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RECENT ADVANCES IN PLANT GENETICS

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Second Edition
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With Foreword by
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Director, John Innes Horticultural Institution

With 55 Illustrations and 49 Tables

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To

PROFESSOR J. MONTAGU F. DRUMMOND

OUR TEACHER AND FRIEND

Printed in Great Britain

FOREWORD

By Sir A. Daniel Hall, K.C.B., M.A., LL.D., D.Sc., F.R.S.,
Director of the John Innes Horticultural Institution, Merton.

The science of genetics is comparatively new, for it may be said to have received its first systematic basis on the general recognition of Mendel's generalisations about the beginning of the present century. Mendel's scheme of inheritance, with its insistence on the transmission from generation to generation of parental characters as units, provided a working basis which served to explain many of the facts that had been observed by the breeders of plants and animals. It also served as a guiding hypothesis to such breeders and enabled them to obtain with some degree of certainty desired combinations of characters and to fix the new types. In the earlier years of investigation exceptions were numerous and only slowly yielded to explanation. Much still remains to be understood, but it may be claimed that all the later work goes to demonstrate the general truth of inheritance on mendelian lines.

De Vries extended the theory by demonstrating that new characters may arise from time to time by "mutations." But the great forward step came with the association of the mendelian characters with the chromosomes of the nucleus, which provided a mechanism on which mendelian inheritance would work and a physical basis for the observed laws of inheritance. In all the more recent work genetical observations are correlated with chromosomal structure and behaviour. Genetics has now become one of the most rapidly developing sciences; the elucidation of the structure of the nucleus is of no less importance than the disclosure of the constitution of the atom. So rapid has progress been that it is difficult for any but professional students to keep in touch with the literature, scattered as the papers are in many different periodicals. There are several excellent handbooks which set out clearly the prime mendelian basis and its explanation by the chromosome theory of heredity. The present book aims at an exposition of the more recent developments of the theory, more particularly within the last ten years, during which the experimental study of polyploidy has done so much to confirm the general hypothesis. The authors are themselves actively engaged in research and are daily brought face to face with the intricate problems that are presented by any exact study of the breeding of plants. They are appreciative of the applications of investigations of this character to creation of the new varieties of plants required by the farmer and the gardener. In that direction indeed lies the greatest promise of economic progress in the production of food, fibre, and other plant materials. In all countries practical men are seeking to create new varieties, this book will give them an outline of the theoretical basis for their work and may save them from many pitfalls and much wasted effort.

A. D. HALL.

PREFACE TO SECOND EDITION

THE present edition of this book has been written under different circumstances from those of the first edition. A considerable number of books, monographs and literature keys have been published since 1932 and information on various subjects is more readily available than formerly. Nevertheless, the spate of new and important work still continues at a phenomenal pace.

The apparent desire for information on recent work expressed by the generous response to the first edition prompts us to retain the literal meaning of "Recent Advances" in the scope of the book. This has necessitated a very considerable re-writing of several chapters (II, III and X) and the remodelling of others, in order to express the newer view-points of geneticists. A chapter on variegation and chimæras has been included, since this subject will become of fundamental importance to genetical theory. The excellent summary of the statistical basis of selection and populations given by Dobzhansky (1938) reduces the need for extensive treatment of this subject here. Therefore the limited space has been used to direct attention to the more biological aspects of genetics, since a common misconception that genetics is a conglomeration of cytological theories, statistical work and peculiar terminology is all too prevalent.

The mass of new work cannot be adequately treated in a small book. Therefore it is thought that a Literature Key with additional references to papers published since the last edition on certain subjects would be helpful to the student. This Key is not intended to be comprehensive but has been found useful in graduate teaching.

It is regrettable that my friend, Dr. Philp, could not co-operate with me in the present edition. Therefore he cannot be held responsible for the views and errors which may be found. The burden of preparation has been considerably lightened by the able assistance of my wife and Dr. L. C. Luckwill, and by an excellent secretary, Mr. J. Stocks. To these individuals and to Messrs. J. & A. Churchill I express my profound thanks.

F. W. SANSOME.

PREFACE TO FIRST EDITION

WHILE there are several elementary text-books on plant genetics, there is no recent book in English dealing with the more modern developments of the science. The present book is an attempt to summarise the chief advances made in plant genetics during the last ten years.

In our choice of matter we have subordinated particular aspects to the wide view. Although of necessity we have had to enter in some detail into particular questions of importance, our principal object has been to give the reader a perspective of modern plant genetics, and the manner in which it has developed and is developing. For this reason we have incorporated much of the work on the fruit fly *Drosophila,* which on certain points provides evidence that is meagre or lacking in plants.

Considerations of space have made it impossible to deal at any length with such questions as sex in plants, chimæras, and the mathematics of inheritance and populations. References to the literature on these subjects, however, are to be found in the bibliography.

The book will, we hope, be useful to the honours student in genetics, but we have intended it primarily for the teacher, the research geneticist (applied and purely scientific) and the general biologist. We may express a hope that this *résumé* of work on the plant side may do a little to remedy the unfortunate lack of contact that exists at present between the plant and animal branches of the science. Many of the phenomena dealt with here, like polyploidy, in spite of the fact that they are of great significance for the general theory of genetics, are at present almost completely ignored by zoologists, as the phenomena are largely peculiar to the plant kingdom.

We take this opportunity of acknowledging our indebtedness to the various authors and publishers who have permitted us to reproduce their figures and tables, and to Sir Daniel Hall, Professor J. B. S. Haldane and our colleagues at the John Innes Horticultural Institution for their help, advice and criticism. Our gratitude is also expressed to Miss D. M. Cayley, Dr. P. Koller, Mr. W. J. C. Lawrence, Mrs. E. Sansome and Mr. L. H. Stone for assistance in proof reading. In conclusion we also wish to thank Messrs. J. & A. Churchill for the manner in which they have placed their experience at our disposal.

F. W. S.
J. P.

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RECENT ADVANCES IN PLANT GENETICS

CHAPTER I

THE MECHANICAL ASPECTS OF HEREDITY

Introduction—Mitosis—Meiosis—Segregation—Interaction of Factors—Inheritance of Pollen Characters — Incompatibility — Lethal Factors — Cytoplasmic Influence.

Introduction. The present edition endeavours to present a summary of the recent investigations and theories relating to the reactions and transmission of inherited characters. The rapidity of the advances made between 1927 and 1932, made the presentation of balanced statements of genetic principles difficult. Now it is possible to make an attempt to separate the essential from the less important features.

In plants there is a more or less well defined alternation of generations. Fertilisation, the fusion of male and female gametes, initiates the sporophyte which gives rise, by the reduction division, to the gametophyte which may or may not give rise immediately to gametes to take part in fertilisation. (See botanical text-books.) The central feature of both fertilisation and reduction is the characteristic behaviour of the nucleus which is constituted by a number of bodies—the chromosomes. These chromosomes undergo changes of appearance throughout their history, but there is strong evidence that they are permanent autonomous bodies. The fusion of two gametes at fertilisation will give rise to a nucleus with the sum of the number of chromosomes contained in the nuclei of these gametes. As the zygote develops, every chromosome divides, so that the daughter cells have a chromosome complement identical with that of the original zygote.

The sporophytic generation thus has, in general, twice as many chromosomes as the gametophytic generation. Immediately before the inauguration of the gametophytic generation, two nuclear divisions take place with only one division of the chromosomes. This process, called meiosis, naturally halves the number of chromosomes.

Where meiosis or, as it is more loosely called, the maturation division or reduction division, follows very shortly after fertilisation as in *Spirogyra*, the diploid state is very short. Where fertilisation follows shortly after meiosis, as in the Angiosperms, the gametophytic generation is of small duration.

Heritable characters must be controlled by determiners, " genes " or " factors," which retain their individuality throughout the life cycle and since, in general, only the nucleus is carried on from generation to generation, these genes are presumably carried in the nucleus.

The discovery of van Beneden in 1883 that the nucleus of the egg and the nucleus of the spermatozoon of *Ascaris* each contained half the number of chromosomes of the nucleus in a body cell, initiated a series of investigations on the physical side of the problem of heredity. Strasburger (1888) showed that the reduction in number of chromosomes took place in the microsporocytes of plants. Weismann and Strasburger independently concluded that the nucleus was " the vehicle of heritable variation " (1884–1885), while Strasburger (1894) postulated that there was a reduction in the number of chromosomes at sporogenesis in all organisms which exhibited sexuality. Rückert (1892) suggested briefly that a conjugation and disjunction of paternal and maternal chromosomes took place at meiosis, while Montgomery (1901*a*,*b*), without the knowledge of Mendel's laws of segregation, emphasised the presence of paternal and maternal homologous chromosomes in diploid groups, and accepted their conjugation and disjunction in pairs at meiosis.

The parallelism between the pairing and disjunction of chromosomes at meiosis and the segregation of inherited characters at the maturation division, was suggested by Strasburger, Correns, Guyer and Cannon about 1901, but Sutton (1903) and Boveri (1904) first clearly realised the significant correspondence between the cytological phenomena and segregation. Boveri (1904), by some remarkable experiments, showed that the development of an organism was influenced by the chromosomes, and that the chromosomes in one organism were qualitatively different in their effect on the characters of the organism.

Much later, Carothers (1913, 1917, 1921, 1926), Wenrich (1917), Navashin (1925*a*,*b*, 1931*a*) and Sveshnikova (1928) have published results independently which demonstrate that the segregation of the chromosomes to the progeny is strikingly similar to that observed for inherited characters.

Carothers (1913, 1917) found that the disjunction of one pair of chromosomes in *Trimerotropis* was not influenced by that of a different pair. It had been known for some time through the work of Wilson *et al.* (see Wilson, " The Cell ") that the pair of chromosomes, which was related to the determination of sexuality, was heteromorphic in many animals. At meiosis, the difference in size or shape enabled observers to see that one chromosome of the pair might pass to one or other of the poles at the first of the two divisions of meiosis (heterotypic), and hence to the daughter cells, while the other member of the pair would go to the alternative pole. It will be seen that a ratio of 1 : 1 in respect of the members of the sex chromosome pair will thus be mechanically obtained for distribution to the daughter cells and the gametes.

Two pairs with heteromorphic members are, however, necessary to prove that disjunction of different pairs of chromosomes is at random and independent.

In *Trimerotropis* Carothers found that in addition to the sex chromosome, which lacked a partner in the male sex (*XO* type), one pair of chromosomes had unequal members, which could be distinguished by their shape and the position of the attachment to the so-called spindle fibre. She found that out of 300 first meiotic divisions 51·3% had the larger member of the dimorphic pair going to the same pole as the sex chromosome and 48·7% had the smaller member of the heteromorphic pair accompanying the sex chromosome. This is remarkably close to the 50% distribution, expected on a random and independent assortment.

Similar observations were furnished by Wenrich (1917) in *Phrynotettix magnus* and by Robertson (1915, 1916) in the *Tettigidæ* and *Acrididæ*. Later Carothers (1917) obtained data involving four different " pairs " of chromosomes in *Trimerotropis fallax*.

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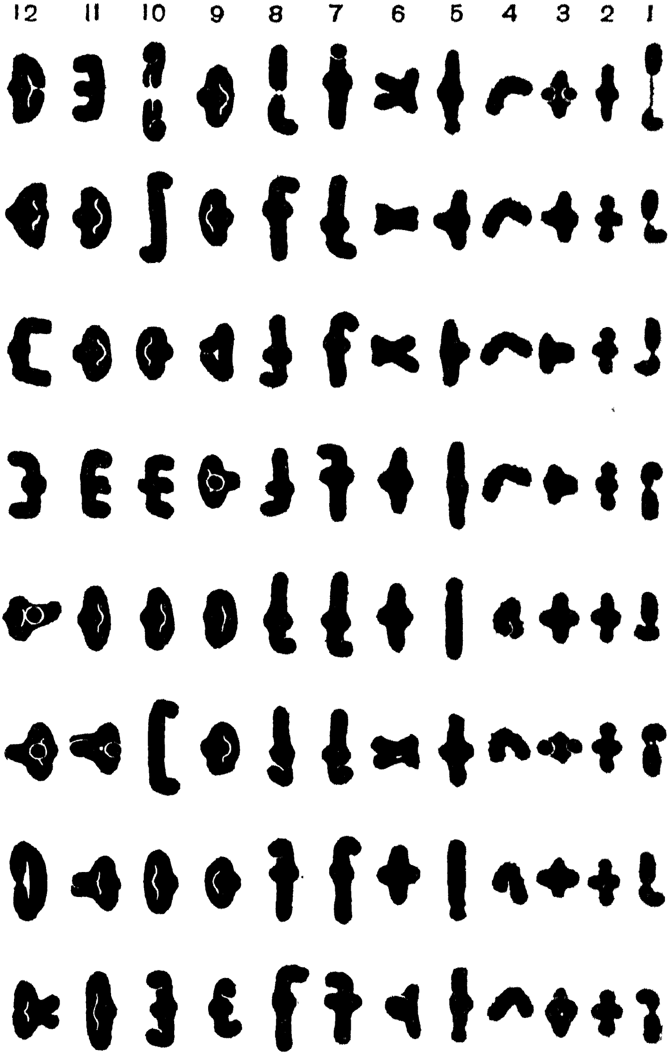


FIG. 1. Lateral views of chromosomes in the first spermatocyte of eight cells from a single individual. The chromosomes of each cell are arranged horizontally in a series according to size. The vertical rows represent the same pair of chromosomes in different cells. Note the difference in shape of separating members in pairs Nos. 1, 7 and 8 and the unpaired sex chromosome, No. 4. (Carothers *ex* Babcock and Clausen, 1927.)

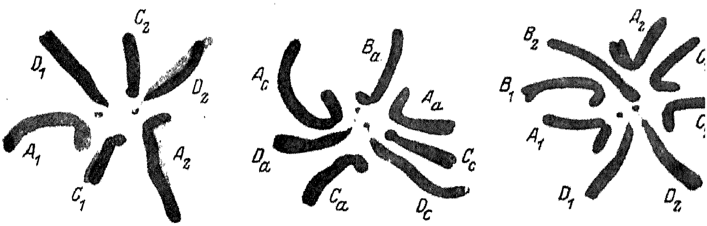


FIG. 2. Somatic chromosomes of (*a*) *Crepis capillaris*; (*b*) F_1 *C. capillaris* × *C. aspera*; (*c*) *C. aspera*. The index letters c and a indicate the parental chromosomes in the hybrid. (Navashin, 1927.)

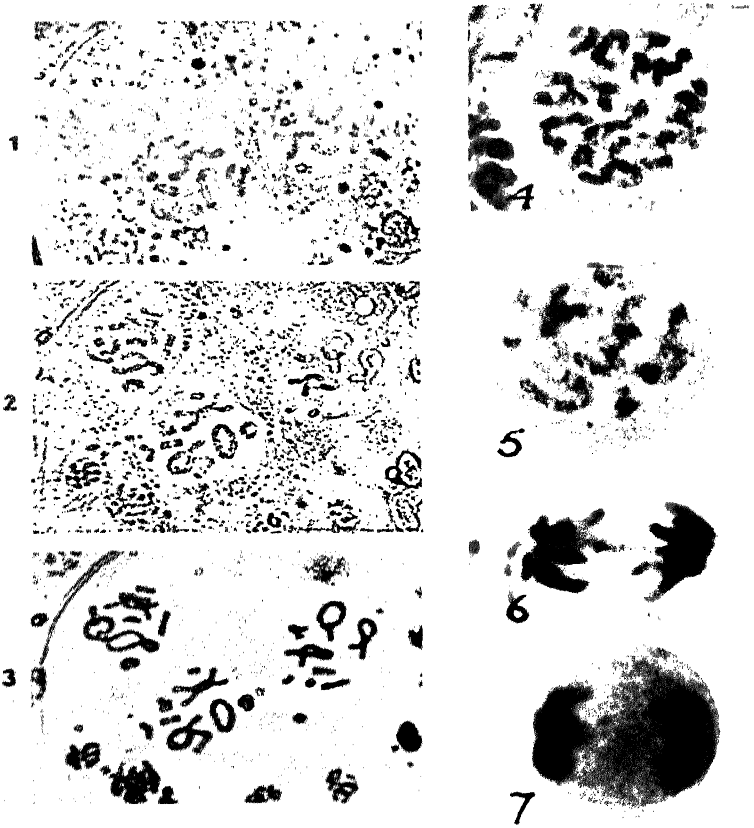


FIG. 3. 1–3. Diakinesis in *Stenobothrus lineatus*. (From Bělař, 1927.) 1. Living cells. 2. The same cells after fixation with osmium tetroxide vapour and Flemming. 3. The same cells after staining with Giemsa-Romanovsky. 4–7. Photographs of living chromosomes of *Melanoplus femur rubrum* (Orthoptera) at meiosis, taken by ultra-violet light. (After Lucas and Stark, 1931.) 4. Late telophase before meiosis. × 1800. 5. Pachytene. × 1800. 6. First anaphase. × 1200. 7. First telophase. × 1200.

[*To face p.* 5.

Table 1, constructed from observations on 100 first divisions (which would give rise to 200 second divisions), shows the closeness between observation and expectation. The chromosomes numbered 1, 7, 8 and 4 (the unpaired sex chromosome) in Fig. 1 were those studied. It will be seen that size and shape difference are pronounced.

TABLE 1. *Distribution of Members of Heteromorphic Pairs of Chromosomes in a Single Individual of* Trimerotropis fallax (*Data from Carothers ex Babcock and Clausen,* 1927).

Type.	Expected.	Observed.
A given V (Nos. 1 or 4)	$\frac{1}{2} \times 200 = 100$	100
Only one V	$\frac{1}{4} \times 200 = 50$	48
Two given Vs (Nos. 1 and 4)	$\frac{1}{4} \times 200 = 50$	46
Two given Vs (Nos. 7 and 8)	$\frac{1}{4} \times 200 = 50$	47
Any two Vs	$\frac{3}{8} \times 200 = 75$	84
Three given Vs (Nos. 1, 7, 8)	$\frac{1}{8} \times 200 = 25$	22
Three given Vs (Nos. 4, 7, 8)	$\frac{1}{8} \times 200 = 25$	21
Any three Vs	$\frac{1}{4} \times 200 = 50$	48
Four Vs	$\frac{1}{16} \times 200 = 12\frac{1}{2}$	8

The chromosome separates from its counterpart which has been derived from a different gamete, and passes to the opposite pole and hence to a different gamete at random. It can be shown in several ways that the chromosome derived from a parent passes into the offspring and is uninfluenced by the passage through the gametophyte.

Navashin (1927*a,b*) crossed *Crepis tectorum,* having eight chromosomes in the somatic tissue, with *Crepis alpina* ($2n = 6$). All the chromosomes can be identified by their shape and size. Gametes were produced by the hybrid ($2n = 7$) with the parental chromosomes (4 and 3), and these could again be recognised in the second generation. The chromosomes had passed through the hybrid and appeared in the succeeding generation without change. Fig. 2 shows that the chromosomes of the parental species *C. capillaris* ($2n = 6$) and *C. aspera* ($2n = 8$) are recovered in the hybrid ($2n = 7$).

In a considerable number of cases the chromosome complement of one species is found to be different from that of a related species. One or more chromosomes may differ in size, or in the position of the attachment constriction or *centromere* (see p. 7), or there may be differences in the number of chromosomes. For example, Navashin, Babcock, Hollingshead and others can recognise the individual chromosomes of *Crepis* and show that there are differences in size, shape and number between different species. In one species the characteristics of the chromosomes are constant, except in those cases where genetic variation is present (cf. Darlington, 1937).

When aberrations occur, such as breaking of chromosomes, it is found that the descendants exhibit the peculiarities expected. For example, the *X* chromosome of *Drosophila melanogaster* was broken into two portions, one of which was attached to the fourth chromosome. In some of the progeny the two half chromosomes were present ; one half was still attached to the fourth chromosome (Stern, 1931).

It will be realised that the nucleus which initiates the new zygote results from the fusion of a paternal and maternal nucleus. The chromosomes thus included in the first cell of the zygote are propagated without qualitative or quantitative change to all daughter cells of the somatic tissue by mitotic division.

MITOSIS

The mechanism of *mitosis* or karyokinesis, was first identified as such by Schneider (1873), Strasburger (1872, 1878), van Beneden (1883), Flemming and others, while the name mitosis, now commonly used, was given by Flemming (1879, 1880, 1882), who showed the characteristic splitting of the chromosomes. The daughter halves of the longitudinally split chromosomes were seen to pass to opposite poles by van Beneden and Heuser about 1884, in animals and plants respectively.,

The zygotic cell of the normal diploid plant contains an even number of chromosomes, each type of chromosome being represented twice. Hence, the chromosome complement of one plant can be separated into two similar sets of chromosomes. One member of each pair of chromosomes has been derived from one parent and the other from the alternative parent.

Description of Mitosis. The nucleus in the resting stage appears to contain a fine network or reticulum, which at the beginning of the division (prophase stage) is resolved into threads, the chromosomes. Each thread appears to be at least double longitudinally along the whole length. The division of each chromosome must have taken place previously to this stage. Considerable disagreement prevails as to the time of the chromosome-split, and as to whether the threads seen at the beginning of mitosis are double, quadruple or octuple in nature (see Darlington (1937), Huskins and Smith (1935), Nebel and Ruttle (1936)). For genetical purposes the question is not of immediate importance. This prophase stage proceeds and the threads shorten and thicken. They become arranged on an equatorial plane in the nucleus and the nuclear membrane disappears. Fine fibres from the poles appear to become attached to a definite position, the centromere, on the chromosomes (metaphase stage). These spindle fibres, which are seen in material which does not show the best fixation, appear to correspond to the highly viscous region found in living material by micro-dissection methods. The fibres are probably fixation products of some (possibly) physical structure of the region.

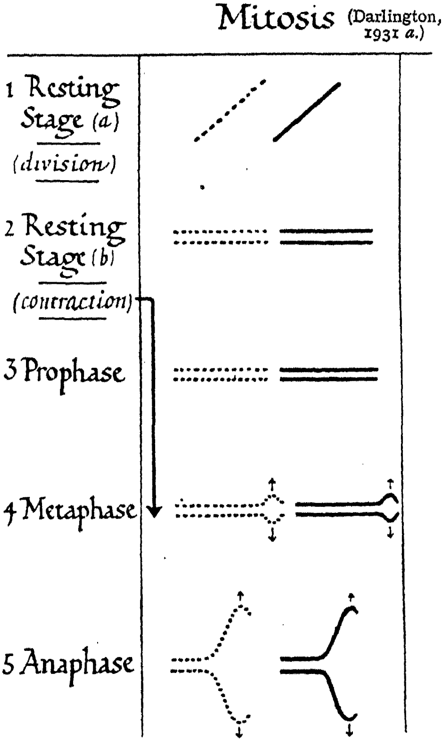

Mitosis (Darlington, 1931 a.)
1 Resting Stage (a) (division)
2 Resting Stage (b) (contraction)
3 Prophase
4 Metaphase
5 Anaphase

FIG. 4.

The paired half chromosomes, or chromatids, separate first at the place where the spindle fibre is attached to the chromosome. This point is generally constricted and is sometimes called the centromere.

Present-day methods of technique have enabled cytologists to determine that these constrictions, as well as secondary constrictions at other places on the chromosome, are constant characteristics of the chromosome. Satellites or trabants which presumably result from a sub-terminal constriction are also diagnostic features of chromosomes. All somatic cells of a normal plant have similar chromosome complements, and it is therefore reasonable to suppose that the chromosome does not lose its individuality during the interphases.

After metaphase the split chromosomes separate and pass to opposite ends of the spindle area (anaphase) and in the Angiosperms, with few exceptions, a cell wall is laid down between the separated nuclei along the spindle fibres, probably by a process of coagulation.

It will be seen, therefore, that during mitosis the chromosome divides into two chromosome parts identical with the original chromosome. At anaphase the two daughter chromosomes are separated in a regular manner and take part in the formation of two daughter nuclei. The complement of chromosomes originally instituted at fertilisation is thus preserved in all living cells of the plant under normal conditions.

Bělăr (1928) made microphotographs of a living cell and of the same cell after fixation and again after staining (Fig. 3). He thus showed that good fixation and staining greatly facilitates the study of the chromosomes without distorting the configurations of the living cell. Further, the processes of mitosis and meiosis have been shown (in living material) to be comparable with those assumed from fixed material.

MEIOSIS

Sexual reproduction, by which most plants produce offspring at some period in their life history, consists essentially in the fusion of two nuclei—the male and female gametes. Since the chromosomes are definite and autonomous bodies, the zygote and the succeeding sporophyte have the sum of the chromosomes contributed by the gametes. If the chromosome number of the species as a whole is to be constant, there must be a process by which the chromosome number is halved during gametogenesis. The place in the life cycle, at which the reduction occurs, varies in different plant phyla. In general, reduction synchronises with the production of spores, in the flower of Angiosperms, on the frond of a fern and in the capsule of a moss.

Meiosis usually consists of two divisions—the first or heterotypic division, in which the reduction of the number of chromosomes takes place, and the second, or homotypic division, in which the products of the first division are propagated as in mitosis. The essential difference between meiosis and mitosis is that in mitosis every division of the nucleus is accompanied by a division of the chromosomes, but in meiosis there are two divisions of the nucleus with one division of the chromosomes. The number of chromosomes is therefore reduced in the resulting nuclei.

Description of Meiosis. For a full description of meiosis reference should be made to Darlington's book in this series. Only an outline sufficient for genetical purposes will be given here.

Diploid Plants. In the early prophase, fine leptotene threads, each representing a whole chromosome are seen to align themselves in pairs (*zygotene* stage).

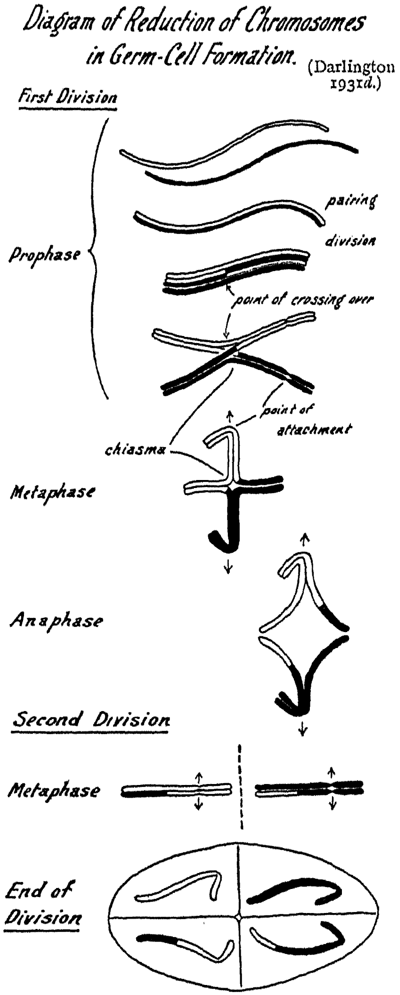
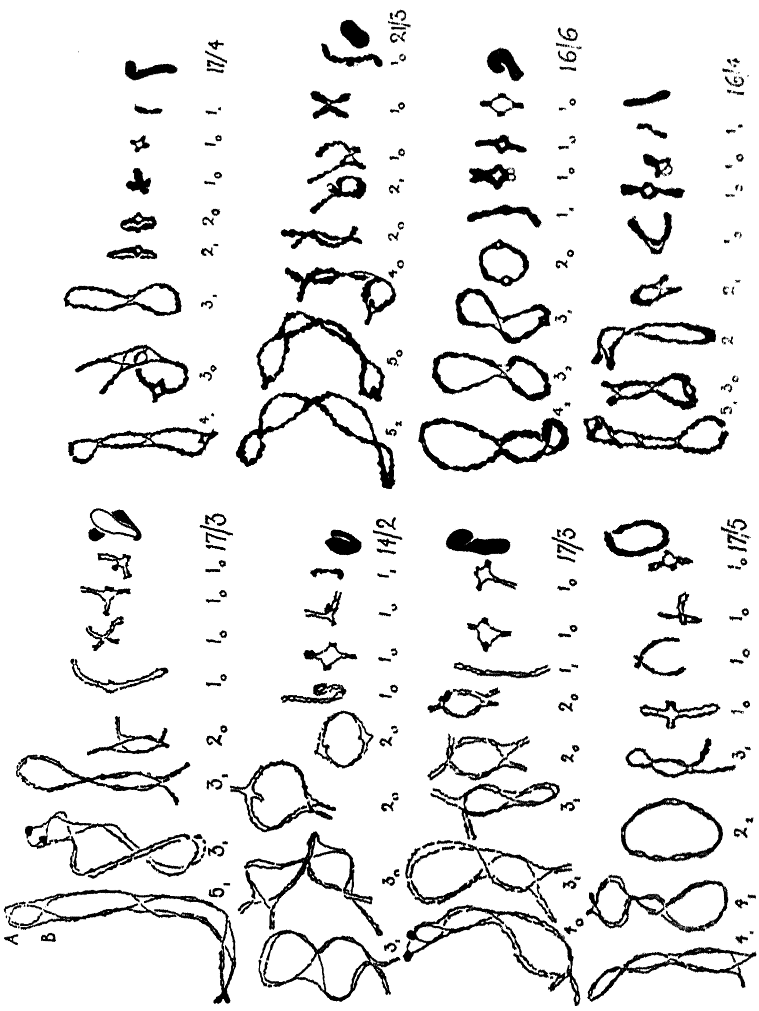


Diagram of Reduction of Chromosomes in Germ-Cell Formation. (Darlington 1931*d*.)

FIG. 5

Each pair of threads represents one chromosome from the paternal parent paired with the corresponding or homologous



chromosome from the maternal parent. The paired threads shorten and thicken (*pachytene*). After the pachytene stage the chromosomes are observed to have split and the resulting chromatids have fallen apart in pairs. The paired chromatids change partners at various points along their length so that the bivalents have a characteristic looped appearance. This stage is early *diplotene*.

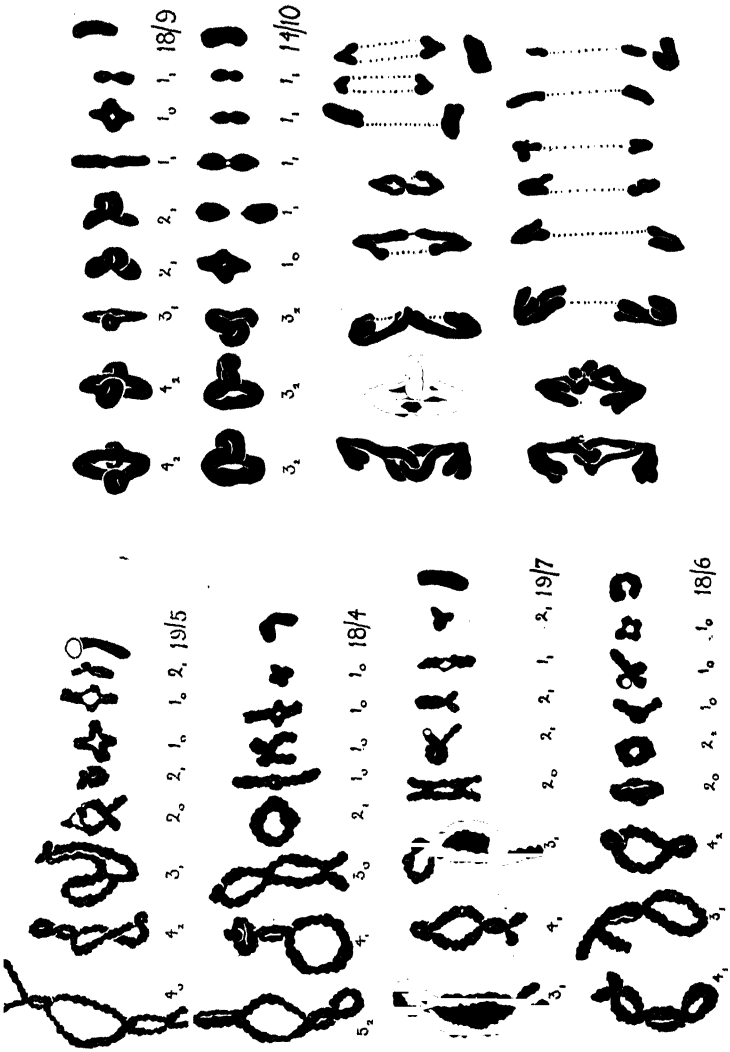


FIG. 6. Meiosis in *Stenobothrus parallelus*. (Darlington and Dark, 1932.)

The changes of partner which are called chiasmata (Janssens, 1907, 1924) are believed to take place in the following way. When the chromosomes split a break occurs in one chromatid which induces a break at the exactly corresponding point in one of the chromatids from the partner chromosome (see p. 83). The broken ends rejoin so that two composite chromatids are formed, each containing parts of the two original chromosomes. When the chromatids fall apart in pairs, chromatids from the same chromosome or identical chromosomes remain associated, with a consequent change of partner at the points where an interchange or crossing-over of chromosome segments has occurred. These changes of partner serve to hold the four chromatids in association as a bivalent. When chiasmata are not formed, bivalent formation also fails.

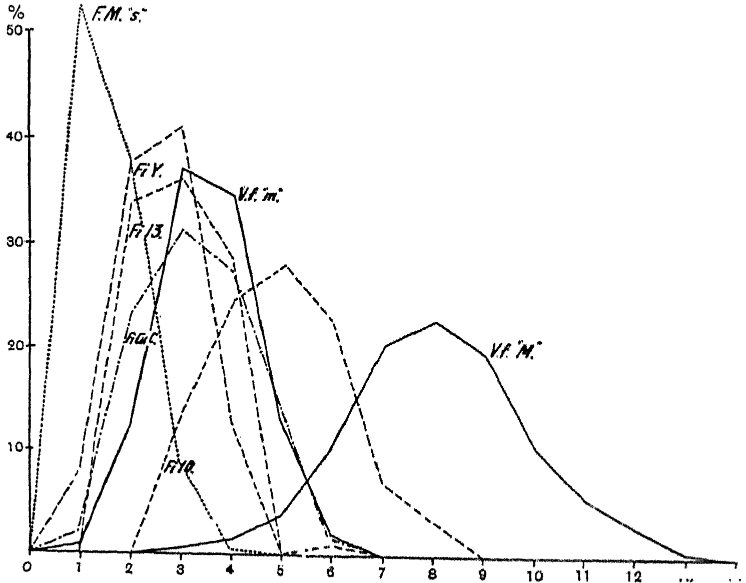


FIG. 7. Chiasmata in *Vicia* and *Fritillaria*. (Darlington, 1931*a*.)

The number of chiasmata is proportional to the chromosome length within certain limits (see later).

The accompanying graph (Fig. 7) from Darlington (1931*a*) illustrates the ranges in chiasmata frequency of chromosomes of different length in *Vicia Faba* (Maeda, 1930*b*), *Fritillaria imperialis* (Darlington, 1930*c*) and *F. meleagris* (Newton and Darlington, 1930). The chiasmata frequencies of the *M* and *m* chromosomes in *Vicia Faba* are entirely different; the *M* chromosome is twice as long as the *m* chromosome. This subject will be returned to in the discussion of genetical crossing-over.

Linear contraction of the four chromatids of a bivalent takes place. At the same time the chiasmata decrease in number to a greater or less extent until the stage of diakinesis, where the bivalents lie at random in the nucleus. Metaphase follows with the arrangement of the bivalents upon the equatorial plate. At anaphase the still undivided centromeres of the original chromosomes pull the attached chromatids to opposite poles of the spindle. Therefore, two chromatids of the bivalent pass to one pole and two to the other (telophase). Telophase is followed by a very short resting stage, and by the homotypic division which is similar to a mitotic division. The previously undivided centromere, holding the chromatids together, splits into two. The two centromeres repel one another, thus pulling the attached chromatids to opposite poles of the homotypic metaphase spindle. Thus the four chromatids formed when the paired chromosomes split at prophase of the first division are distributed to four nuclei which usually initiate the gametophytic generation. In the flowering plants, these four nuclei become the pollen nuclei on the male side, and on the female side one of them usually functions to produce the embryo sac.

It is generally accepted that the chiasmata formed at early diplotene hold paired chromatids together until metaphase. During the early stage these chiasmata may move along the chromosome length from the position where they were first formed. Usually this movement is towards the ends of the chromosomes, where successive chiasmata may replace one another. This phenomenon of *terminalisation* reduces the number of chiasmata between diplotene and metaphase. The terminalisation coefficient $\frac{\text{No. of terminal chiasmata}}{\text{total chiasmata}}$ has been used as a measure of terminalisation, but its value is limited. Where terminalisation does not occur to any extent as in *Pisumsativum* and *Fritillaria meleagris* the anaphase configurations reflect the previous exchanges of partners of the chromatids at prophase.

Lately much work on the spiral structure of chromosomes in relation to the mechanics of their behaviour has been published. It is not necessary for genetical purposes, however, to enter into the details of the many cytological theories relating to meiosis. (See Sax (1936) for a balanced treatment.)

MEIOSIS IN POLYPLOIDS

The cytological investigation of forms with more than two sets of homologous chromosomes has been productive of much value

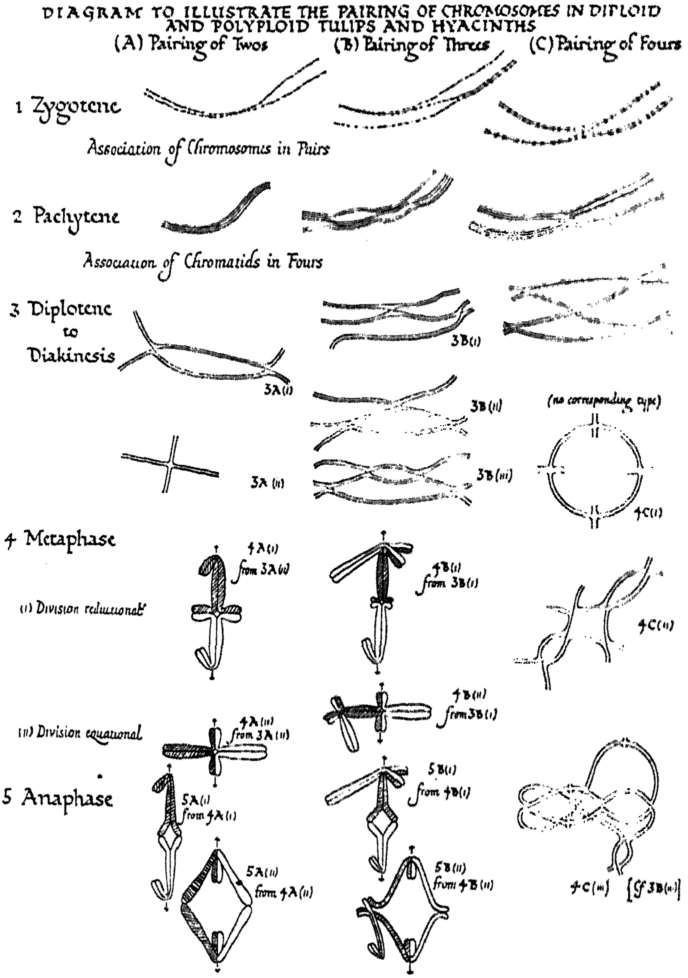


FIG. 8. (Darlington, 1929*b*.)

in the hands of Belling and Darlington and others. In a normal diploid plant each maternal chromosome has a paternal homologue but in a polyploid there may be more than two homologues present.

In these forms trivalents (three chromosomes), quadrivalents (four chromosomes) and associations of greater numbers of homologous chromosomes may be found (see Fig. 8). The important and fundamental point is that *never more than two chromosomes are associated at any one point.* Pairing between two chromosomes at one point may not greatly influence pairing between one member of this association and a different chromosome at another point (see later and Mather, 1938, for a fuller discussion). Hence, in a triploid, two chromosomes may be in association at one point, while at another point one may be involved with a third. After zygotene pairing between chromosomes two at a time, chiasmata are formed between the paired parts. Both qualitative and statistical analyses are being made on the behaviour of chiasmata with interesting and important results (see p. 88).

CHROMOSOME DISJUNCTION AND SEGREGATION

Segregation depends on the disjunction of the chromosomes at the first division and the separation of the chromatids at the second division of meiosis. Disjunction of the members of a bivalent will naturally be regular and only exceptionally will both members of a bivalent pass to one pole after pairing (non-disjunction).

Normal disjunction is less certain, however, in trivalents, quadrivalents and higher associations of chromosomes. Indeed in a form such as a triploid, with an odd number of homologous chromosomes disjunction will always be irregular. In such a case the three chromosomes will either become associated and disjoin two to one pole and one to the other, or a bivalent and univalent may be formed, which again give rise to a distribution of two and one. There is considerable difficulty in giving a convenient terminology to these cases for descriptive purposes. Non-disjunction implies that the members have paired at prophase and have passed to the same pole. Neither of the above triploid cases, however, may be true non-disjunction, since the chromosomes concerned may not have paired at all. When the trivalent is formed one may find that chromosome *B* pairs with the homologues *A* and *C* in different parts of its length and that *B* goes to one pole and *A* and *C* go to the other.

A and *C* have not paired at prophase *inter se*, but are controlled by their associations with *B*.

Disjunction, non-disjunction and numerical irregular distribution must be distinguished, since they have distinct genetical consequences with regard to segregation. This will be referred to again under triploid and tetraploid segregation.

SEGREGATION

We have seen that the chromosomes within the nucleus are transmitted without change from cell to cell in the somatic or body tissue, and that their pairing and reduction in meiosis is a characteristic phenomenon associated with the initiation of the gametophyte leading to gamete formation. It may be shown in several ways that the chromosomes carry determiners or " genes " which control the transmission and behaviour of inherited characters.

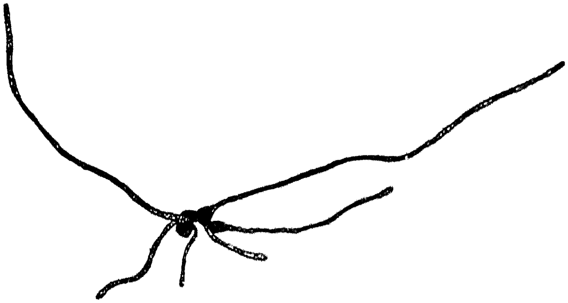


FIG. 9. *Funaria hygrometrica univalens macrospora* × *microspora*. Germinating tetrad of spores. × 40. (Wettstein, 1924*a*.)

Indeed, it is now possible, by combining cytological and genetical analysis in *Zea*, *Drosophila*, *Datura*, *Lycopersicum* and other organisms, to identify chromosome parts, which, through their gene content, have control over the inheritance and behaviour of specific morphological characters. It will be shown that each part of a chromosome is qualitatively different from every other part in respect of the effect on the development, physiology and morphology of the plant. This effect is due to the so-called genes carried on the chromosomes. It has been shown that the paired chromosomes disjoin from one another at meiosis in a regular manner on a random basis, and that the cells resulting from the meiotic division will contain 50% of the one partner and 50% of the other—1 : 1 ratio. It is possible to show that inherited characters segregate in a similar manner. Wettstein (1924*a*) crossed two races of *Funaria hygrometrica,* which differed in a number of characters, including the rate of growth of the protonema. A hybrid sporophyte thus formed by fertilisation contains genes from both races. The spores from such a hybrid were found to remain together in fours and to give, on germination, two quickly growing and two slower growing protonemata in each set of 4 spores (see Fig. 9) (1 : 1 ratio). These spores are the immediate descendants of a cell in which meiosis has occurred. This segregation of rate of protonema growth is similar to the manner in which chromosomes are segregated at meiosis. The races which were hybridised also differed in a number of characters; large spore **G**, high rate of division in the protonema **O**, broad perichætial leaf **B**, shape of the paraphysis cells **P**, coloured capsule **C**. The cross made between the two plants of the genetic constitutions **GOBPC** and **gobpc** gave eight similar sporophytes which must have had the constitution **GgOoBbPpCc**. Wettstein isolated 62 spore tetrads of which 41 germinated and after fertilisation 35 formed mature sporogonia.

In all the tetrads of spores it was found that only two types of spores occurred in any one tetrad. Thus in 24 tetrads

16 gave 2 spores with **GBPC** and 2 with **gbpc**
5 ,, ,, ,, ,, **GBPc** ,, ,, ,, **gbpC**
2 ,, ,, ,, ,, **GBpc** ,, ,, ,, **gbPC**
1 ,, ,, ,, ,, **GbPc** ,, ,, ,, **gBpC**

and in 11 tetrads

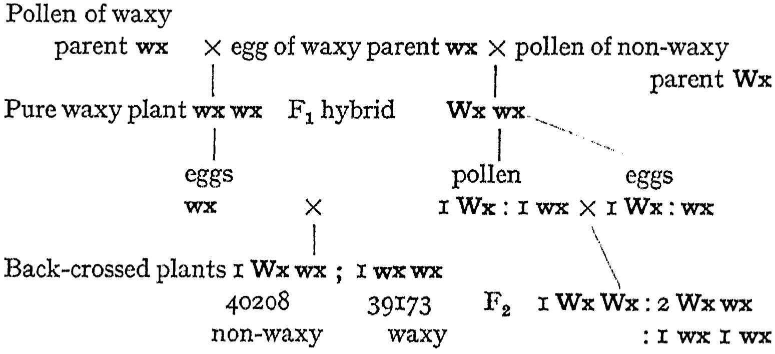
6 gave 2 spores with **GBPC** and 2 with **gbpc**
1 ,, ,, ,, ,, **GBPc** ,, ,, ,, **gbpC**
1 ,, ,, ,, ,, **GBpC** ,, ,, ,, **gbPc**
2 ,, ,, ,, ,, **GbpC** ,, ,, ,, **gBPc**
1 ,, ,, ,, ,, **GbPc** ,, ,, ,, **gBpC**

Tetrad Analysis. The analysis of the gametophytic generation in mosses, ferns, fungi, algæ, and to some extent in angiosperms (Michaelis (1931) and p. 102), provides fundamental evidence of the time and place of the segregation of genes. While the analysis is laborious and rarely of statistical value, the demonstration is important in showing that the immediate products of meiosis are qualitatively different in respect of one pair of alternative (allelomorphic) characters; that segregation has taken place during meiosis, and that each pair of alternative characters behaves as a unit distinct from every other pair of contrasting characters. Further, the parental types are recovered in the progeny without change or contamination by the transmission through the sporophytic generation. It is possible in various organisms to determine at which of the two divisions of meiosis particular pairs of allelomorphic characters segregate. Consider the pairs of allelomorphic characters **Gg** and **Bb** in Wettstein's case above. In all spore tetrads examined only two types of spores were found in any tetrad—either **GB** and **gb**, or **Gb** and **gB**. This indicates that in both pairs of characters, segregation of **G** from **g** and **B** from **b** has occurred at one and the same division of meiosis. Fig. 12 and 13 shows that if one pair of allelomorphs segregates at the first division of meiosis and the other at the second division, four types of spores will be found in one tetrad.

Mendelism. As a result of studying the segregation of characters in the progeny of hybrids between races of garden peas, *Pisum sativum*, Mendel postulated two laws of inheritance in 1865. These expressed in Mendel's words (translation of Bateson, 1930) are "the theory is confirmed that the pea hybrids form egg and pollen cells, which in their constitution represent in equal numbers all constant forms which result from the combination of the characters united at fertilisation," and "the relation of each pair of different characters in hybrid union is independent of other differences in the two original parental stocks."

The laws may be understood by considering several examples. Brink and McGillivray (1924) and Demerec (1924 *a*) independently showed that the pollen of a race of maize, called waxy, stained red in iodine, while that of non-waxy races gave the characteristic blue reaction of starch in iodine. The hybrids, "F_1," resulting from a cross between these races produced pollen of which 50% stained red and 50% stained blue in iodine. Demerec gives the figures 3,437 blue staining pollen-grains and 3,482 red staining pollen-grains, while Kieselbach and Petersen (1926) give further counts of 13,014 blue staining and 13,229 red staining grains. In percentages Kieselbach and Petersens' results are 49·59% blue and 50·41% red.

The contrasting characters, waxy and non-waxy, of the two races are combined in the first filial (F_1) generation hybrid. This hybrid, "heterozygous" for the two characters, gives pollen (and eggs), half of which contains one character and half contains the other character, a 1 : 1 ratio of waxy to non-waxy pollen (or eggs). The characters have been passed through the hybrid plant to appear in an unchanged condition in the pollen (and eggs) of the F_1 hybrids. The endosperm of waxy and non-waxy races also differs in the starch content, therefore an experiment can be devised to follow the transmission of the character from the pollen grain to the endosperm. Kieselbach and Petersen fertilised a pure waxy maize plant with pollen from an F_1 hybrid between waxy and non-waxy. Among 18,549 fruits 51·56% had waxy endosperm and 48·5% had non-waxy endosperm. These authors summarised the results obtained by Kempton, Bregger and Brink on endosperm segregation in maize and showed that from 203 ears of maize, 39,173 out of 79,381 fruits had waxy endosperm, *i.e.*, 49·3% waxy and 59·7% non-waxy. If we symbolise waxy by **wx** and non-waxy by **Wx** we may illustrate the segregation by the following diagram.


Pollen of waxy
parent **wx** × egg of waxy parent **wx** × pollen of non-waxy
parent **Wx**
Pure waxy plant **wx wx** F_1 hybrid **Wx wx**
eggs
wx ×
pollen
1 **Wx** : 1 **wx** × 1 **Wx** : **wx**
eggs
Back-crossed plants 1 **Wx wx** ; 1 **wx wx**
40208
non-waxy
39173
waxy
F_2 1 **Wx Wx** : 2 **Wx wx**
: 1 **wx** 1 **wx**

The authors also inbred the hybrid F_1 plant **Wxwx** which gives eggs carrying the **Wx** and **wx** characters in the same ratio (1 : 1) as the pollen. The diagram also indicates the resulting combinations which are produced at fertilisation in a ratio of 1 **WxWx** : 2 **WxWx** :

1 **wxwx**, or three plants (75%) carrying **Wx** to one (25%) carrying **wx**. The actual numbers found were 112,248 carrying non-waxy: 36,523 carrying waxy in 356 ears or 23·9% in place of the 25% expected. (This point will be considered on p. 35.)

Parnell (1921) and Chao (1928*a*) found a similar segregation in *Oryza sativa*. From the self-fertilisation of hybrid plants resulting from starchy × non-starchy plants of rice 57,925 fruits were produced of which 44,043 had starchy endosperm and 13,882 had non-starchy endosperm.

The transmission of the characters obviously must depend on some physical unit which is carried in the nucleus. These units are now called *genes* (or character determiners). In the above example the genes **Wx** and **wx** are contributed by the parental races to the hybrid and pass through the pollen and eggs to the succeeding generations. Also, as pointed out by Mendel, the pollen and eggs each contain only one gene of the pair of genes present in the diploid plant. The terms personified gamete or "purity of the gamete" have been used to express this conception, but for several important reasons this view is of less importance to-day.

It will be noticed that the starchy endosperm in rice and the non-waxy endosperm in maize predominate in the F_2 generation (75% : 25%). The fruit of the hybrid plants of this generation containing genes for waxy and non-waxy (**Wxwx** in maize) is similar in appearance to the non-waxy fruit of the parent **WxWx**. This phenomenon is known as dominance. **Wx** is said to be *dominant* to the *recessive* **wx**. Various degrees of dominance may be shown between allelomorphic genes. It was thought by some of the earlier workers in genetics that the characters and genes were closely connected or even synonymous. The phrase "unit character" used in place of gene was adopted to indicate that for every heritable character exhibited by the plant there was an "id," "pangen" or unit which was transmitted through the gametes. This doctrine possibly arose under the influence of Weismann's idioplasm doctrine that the germ plasm contained a factor for every inherited characteristic of the organism. This view was soon realised to be false. On the one hand several genes ("complementary factors") were found to be necessary to produce a certain character while, on the other, one gene ("pleiotropic factor") could affect several characters.

Where there are two pairs of contrasting characters such as tallness *v.* dwarfness and red *v.* yellow fruit in the tomato, the segregation of each pair may be independent of the other pair. Suppose, for example, a tall red-fruited tomato is crossed to a dwarf yellow-fruited tomato plant. The hybrid will contain genes of all four characters **D**, **d** and **R**, **r**. Each pollen grain or megaspore of the hybrid will contain either **D** or **d** and **R** or **r** (the ratio of 1**D** : 1**d** and 1**R** : 1**r** being observed). Hence pollen or eggs will be formed in the ratio of 1**DR** : 1**Dr** : 1**dR** : 1**dr**. This phenomenon of independent segregation of two pairs of genes can be followed in the fern.

TABLE 2

	AB $1-p$	**Ab** p	**aB** p	**ab** $1-p$
AB $1-p$	**AABB** $(1-2)^2$	**AABb** $p(1-p)$	**AaBB** $p(1-p)$	**AaBb** $(1-p)^2$
Ab p	**AABb** $p(1-p)$	**AAbb** p^2	**AaBb** p^2	**Aabb** $p(1-p)$
aB p	**AaBB** $p(1-p)$	**AaBb** p^2	**aaBB** p^2	**aaBb** $p(1-p)$
ab	**AaBb** $(1-p)^2$	**Aabb** $p(1-p)$	**aaBb** $p(1-p)$	**aabb** $(1-p)^2$

Andersson-Kottö (1927) bred from one plant of the fern *Polystichum angulare*, and cultured the prothalli (gametophytes) resulting from each spore separately. Fertilisation between the ovum and spermatozoid of a prothallus again gives rise to the sporophytic generation. She found that there were four types of plants in respect of frond development (types 1, 2, 3, 4). After isolating the prothallus arising from each spore separately and only permitting self-fertilisation each type occurred with approximate equal frequency: Type 1, 22; Type 2, 20; Type 3, 18; Type 4, 18. Andersson-Kottö was thus able to analyse the nature of the genes for frond type which were carried but not exhibited by the prothallus. If the original plant was of the constitution **AaBb**, where **A**, **a** and **B**, **b** are two pairs of allelomorphic genes, the reduction division which will give rise to the spores and resulting prothalli will separate **A** and **a** and **B** from **b** to give the combinations **AB**, **Ab**, **aB** and **ab** in the ratio of 1 : 1 : 1 : 1. Self fertilisation of each prothallus will only produce pure type sporophytes **AABB**, **AAbb**, etc.—in the same ratio to give the four types found. Type 1 requires the presence of two genes **AB**, Type 2 only requires **A**, Type 3 only requires **B** and Type 4 requires neither **A** nor **B** to be present to induce their respective characteristics.

Random fertilisation was also permitted between the gametes of the prothalli of constitutions **AB**, **Ab**, **aB**, **ab**. As a result a ratio of 9 Type 1 ; 3 Type 2 ; 3 Type 3 ; 1 Type 4 sporophytes was obtained. This ratio is that usually found when two pairs of allelomorphic genes segregate in the F_2 generation. There are sixteen ways in which the four types of gametes may mate (see Table 2). The expected properties may also be found by multiplying the gametic ratio (1**Ab** : 1**aB** : 1**Ab** : 1**ab**) by itself algebraically thus arriving at the zygotic ratio resulting from the contributing gametic ratios.

Conclusions. Several definite conclusions may be drawn from the foregoing experiments. In the sporophyte, with a diploid constitution, factors controlling character inheritance are present in duplicate ; either there may be two identical allelomorphs, or in hybrids two different allelomorphs. These separate from one another at meiosis as self-propagating units uninfluenced by their association together. The resulting haploid generation contains one representative of each pair of allelomorphs. The expectation of a 1 : 1 ratio of segregation is found.

As postulated by Mendel, the gametes of a normal plant or animal are pure (but see p. 177) for one member of each pair of allelomorphs. Further, each pair of allelomorphs segregates independently of other pairs (but see p. 73). By random mating of the gametes produced in the definite 1 : 1 ratio in respect of two allelomorphs, it is expected that the resulting zygotes will be formed in definite and corresponding proportions. Thus by selfing a plant which produces gametes containing factors **A** and **a** in the ratio 1 : 1 we expect the progency to be in the ratio of $(1\mathbf{A} : 1\mathbf{a})^2$ or 1**AA** : 2**Aa** : 1**aa**.

INCOMPLETE DOMINANCE

Some characters, such as distribution of colour in the flower of *Primula sinensis*, are not completely dominant. There are two factors **D** and **G** which suppress colour in the petals of *P. sinensis*. **G** makes the gynœcium green and inhibits the expression of colour in the centre of the petals. **D** inhibits colour on the periphery of the flower. Therefore a plant with the factors **DG** will have white flowers. In plants with red stigmas, *i.e.*, with the recessive factor **g** instead of the dominent **G**, it is found that these plants **DDgg** have a coloured centre to the flower, the so-called "Duchess" type, **ddgg** flowers are pigmented throughout while **Ddgg** is flushed at the edges, the so-called "General Buller." Thus it is seen that plants of the constitutions **DD** and **Dd** are different in appearance, due to the fact that **D** is not completely dominant over **d**. If we cross two heterozygous plants **Ddgg** (General Buller) together, we obtain progeny in the ratio of 1 Duchess **DDgg** : 2 General Buller **Ddgg** : 1 fully pigmented plant **ddgg**.

INTERACTION OF FACTORS

Complementary Factors. Bateson and Punnett crossed two plants of "Emily Henderson," a white-flowered variety of sweet pea (*Lathyrus odoratus*), and obtained an F_1, all of which had red flowers. On selfing this F_1, the F_2 progeny segregated into nine coloured and seven white-flowered plants. It was found that two dominant factors **C** and **R** were required to be present together to produce colour, and when only one or neither was present no colour was produced. Hence the F_2 would segregate in the ratio 9**CR** : 3**Cr** : 3**cR** : 1**cr** (see chequerboard, Table 2), of which only the first group would be coloured. These factors **C** and **R** are called "complementary" factors.

It was found that another factor **Bl** converted the red colour of **CR** plants into purple but did not affect the white flowered plants. An F_2 from the crossing of plants with the constitutions **CCrrBlBl** and **ccRRblbl** (both white-flowered) segregated in the ratio of

27 purples : 9 reds : 28 whites. The factorial scheme can be summarised therefore as follows:—

CRBl purple, **CRbl** red and other constitutions white.

The following examples are quoted to direct attention to the subject of complementary factors, a full account of which is given by Matsuura (1933), Onslow (1925) and Scott Moncrieff (1936).

In *Matthiola incana*, Tschermak (1912) and Saunders (1928*b*) found two complementary factors **C** and **R** for red sap colour. Other factors modified the expression of **C** and **R**. Two factors **H** and **K** were necessary for the production of hoariness, but these factors were only effective in the presence of **C** and **R**.

Blakeslee (1921*b*) found that there were two different yellow bud cones in races of *Rudbeckia*, which, when intercrossed, gave a ratio of 9 purple : 7 yellow in the F_2, indicating that two complementary factors were segregating. On treatment with potassium hydroxide, he found that one type of yellow turned black while another turned red. Hence by testing the F_2 progeny he separated the yellow group into a ratio of 4 which turned red to 3 which turned black. In other words, by chemical means, Blakeslee was able to identify those yellows which carried one of the complementary factors for purple.

In *Antirrhinum majus*, Baur (1910, 1911) found that ivory-flowered plants when crossed to certain white-flowered plants give a magenta F_1 and a ratio of 9 magenta : 3 ivory : 4 white in the F_2.

Here, therefore, one of the dominant factors, even in the absence of the dominant member of the other pair, affects the character expression (ivory). Similarly, the cross yellow-flowered × certain white-flowered plants gives a red F_1 and a ratio of 9 red : 3 yellow : 4 white plants in the F_2.

In maize four factors **CRAPr** produce the full purple-coloured aleurone layer in the fruit, East and Hayes (1911) and Emerson (1918).

The progeny of a plant heterozygous for three factors **C**, **R** and **A** segregates in a ratio of 27 coloured to 37 colourless, indicating that these three factors are complementary for colour. This phenomenon, where two or more non-allelomorphic factors affect the same character, is of frequent occurrence in plants and animals. One factor such as **Pr**, which converts the red colour of **CRA** into purple, may suppress the characteristic expression of these non-allelomorphic factors. Such a factor is epistatic to the hypostatic **CRA** factors (Bateson, 1930). One factor may modify without completely suppressing the expression of another factor. Such a factor is called a modifying factor. For example, Fraser (1924) found that the intensity of colour depended on a factor " **In** " the presence of which lightened the shade of colour produced by the factors **CRAPr** or **CRApr**. Hence the factors for aleurone colour are :—

CRAPrIn light purple,	**CRAprIn** light red,
CRAPrin dark purple,	**CRAprin** dark red,

all other combinations being colourless.

East and Hayes have shown also that the presence of an inhibiting factor **I** prevents the formation of colour in the aleurone layer even when **CRAPr** are present. Emerson (1918) points out that the expression of colour in the aleurone grain layer is also influenced phenotypically by endosperm characters, which are controlled by factors independent of those mentioned. For example, with waxy endosperm the purple colour of **CRAPr** appears a dull black.

Kvakan (1924) added **Bn**, the factor for Brown aleurone to the factors involved in aleurone colour. When the endosperm is colourless, due to absence of **CRA**, the caryopsis is yellowish in the presence of **Bn**, but in the presence of **CRA** the aleurone assumes the brown characteristic. **Bn** is unrelated to the other factors in the development of colour in the aleurone. Thus **I** does not inhibit the expression of **Bn**.

The complex interaction of factors is further illustrated by colour inheritance in the vegetative parts of maize. Three fundamental factors are involved. **A**, the factor already seen in connection with aleurone colour, is necessary for the production of anthocyanin, chrysanthemin (Sando, Milner and Sherman, 1935). **Pl** converts the red of **A** plants to purple, and **B** gives rise to a flavone (brown) isoquercetrin. The scheme is therefore

ABPl purple,
ABpl sun-red,
AbPl dilute purple,
Abpl dilute sun-red,
aBPl brown,

all other combinations green.

Hence a cross, **ABPl** × **abpl** will produce in the F_2 a ratio of 27 purple : 9 sun-red : 9 dilute purple : 9 brown : 3 dilute sun-red : 7 green plants. *Cf.* Table 3 for the results obtained by Emerson (1921 *b*).

The backcross of the F_1 to the bottom recessive **abpl** will segregate in the ratio of 1 : 1 : 1 : 1 : 1 : 3 of the above categories.

TABLE 3 (compiled from Emerson's results).

Cross.	Purple.	Sun-red.	Dil. purple.	Dil. sun-red.	Brown.	Green.	Total.
AaBbPlpl ×	obs. 952	305	275	91	278	216	2,117
AaBbPlpl	exp. 893	298	298	99	298	232	
AaBbPlpl ×	obs. 170	160	176	160	172	479	1,317
aabbplpl	exp. 165	165	165	165	165	495	

Dilute sun-red can be of two constitutions, **AA** or **Aa** with **b** and **pl** in the recessive condition, and brown can be of four constitutions, **BBPlPl**, **BbPlpl**, **BbPlPl** or **BBPlpl**, together with the recessive **a**. The cross, dilute sun-red × brown will therefore give rise to a definite series of ratios, depending upon the constitutions of the parents used.

Emerson found that nine crosses of this type produced all purple offspring. The constitutions of the parents were therefore dilute sun-red **AAbbplpl**, and brown **aaBBPlPl**.

Seven crosses of this type produced 143 purple (**AaBbPlpl**) and 147 sun-red (**AaBbplpl**), therefore the parents were dilute sun-red **AAbbplpl** and brown **aaBBPlpl**. Six crosses of this type gave 105 purple (**AaBbPlpl**) and 123 dilute purple (**AabbPlpl**). The parents were therefore dilute sun-red (**AAbbplpl**) and brown (**aaBbPlPl**). Four crosses gave 9 purple : 11 sun-red : 19 dilute purple : 17 dilute sun-red, therefore the parents were of the constitution, dilute sun-red (**AAbbplpl**) and brown (**aaBbPlpl**).

It will be seen that although the phenotypes of the brown plants were alike, the genotypes were different and gave different products when crossed to dilute sun-red.

These results obtained by Emerson are extremely interesting and useful for the study of normal mendelian segregation of more than one factor. Emerson has tested out all the possibilities by intercrossing plants with the different constitutions, and has obtained confirmatory evidence of the correctness of this factor hypothesis.

In carrying out this work he was also able to show that there was a multiple allelomorphic series, of which **R**, one of the factors concerned with aleurone colour inheritance, was one member. These allelomorphic factors affect the expression of **APBl** plants, and also several other combinations. For example, **Rr** and **rr** give pink anthers. Both are dominant to the allelomorphs **Rg** and **rg**, which give green anthers. Emerson found that plants which were normally dilute purple or dilute sun-red were green in presence of homozygous **RgRg**, but in the presence of **Rr** or **rr** they were normal.

The most remarkable feature of this allelomorphic series is that a single factor behaves as a dominant to another of the series in respect of colour in one part of the plant, while in another part of the plant the same factor is recessive. Thus Emerson obtained the following results :—

Rrg gives green anthers and silks in all coloured plants except brown plants.
Rg and **rg** give green anthers and silks in purple and sun-red plants, and also give green plants in dilute sun-red and dilute purple plants.
Rch intensifies brownish purple and dilute purple probably through its action on the factor **B**,
Rr is dominant for aleurone and plant colour,
rg is recessive for aleurone and plant colour,
rr and **rch** are recessive for aleurone colour and dominant for plant colour,
Rg is dominant for aleurone colour and recessive for plant colour,
Rrg is dominant for both, but recessive for anther and silk colour.

In *Primula sinensis* there are at least seven main factors which must be present in the dominant condition to give the normal leaf shape (palmate) to the plant. The recessive allelomorphs that have been identified by a characteristic expression of the leaf character are " fern," " tongue," " oak," " maple," " claw " and two different factors which crimp the leaf. (Gregory, de Winton and Bateson (1923) and de Winton unpub.). In *Pharbitis Nil*, Imai (1926–1931) finds that it is necessary for seven fundamental factors and three modifiers to be present as dominants, together with the recessive allelomorph of "Blown," in order that the normal leaf shape may be obtained. The recessives of the seven fundamental factors are "dragonfly," "cordate," "maple," "willow," "polymorphic," "acuminate," and "pear":—named according to the effect on the character of the leaf. Among these recessives it is found that dragonfly is hypostatic to both cordate and maple, and cannot be recognised in their presence. There is also a dragonfly suppressor which as a dominant inhibits the dragonfly recessive's action. Both in *Primula sinensis* (Anderson and de Winton, 1935) and *Pharbitis Nil* these factors which have been identified by their effect on the leaf, influence the characters of other parts of the plant, and in particular the shape of the petals. For example, the willow factor in *Pharbitis* produces narrow cotyledons and petals and makes the plant female sterile, while maple divides the normally gamopetalous corolla into five cut segments. Obviously there will be many other factors in *Primula* and *Pharbitis* which control the development of the leaf.

Imai (1931*a*,*b*) has summarised the known facts regarding flower colour in *Pharbitis Nil.* Besides three factors, $\mathbf{W_1}$, $\mathbf{W_2}$ and $\mathbf{W_3}$, of which $\mathbf{W_1}$ and $\mathbf{W_2}$ are complementary for colour, the recessive factor **pr**, converts a blue into purple, and **mg** converts a blue into magenta, while $\mathbf{prmgW_1W_2}$ is red. There is a factor **dy** which gives a dusky flower; this factor is hypostatic to **dk**, which gives a duskish flower. Governing flower tones, there is a factor, **i**, which intensifies colour, and two factors, $\mathbf{lt_1}$ and $\mathbf{lt_2}$, hypostatic to **i**, which lighten colour. Dilute **D** is a dominant which reduces colour, while the factor for tinged is a recessive which also reduces colour intensity.

In *Pharbitis Nil*, Imai (1921) and Hagiwara (1923) (see Matsuura, 1929) found that the cross, red-stemmed white flower × green-stemmed white flower gave a coloured F_1 and a ratio of nine coloured to seven white-flowered plants in the F_2. Two complementary factors, **C** and **R**, are therefore concerned in colour production. In addition, three other factors, **A**, **Pl** and **B**, are concerned in modifying this colour, thus:—

CRAPlB	blue.
CRAPlb	purple.
CRAplB	purple.
CRAplb	scarlet.
CRaplB	dark red.
Cr,cR and **cr** combinations	white.

In the neighbouring species, *Pharbitis purpurea*, Barker (1917) found two complementary factors, **C** and **R**, for colour production.

In *Portulaca grandiflora*, Yasui and Ikeno (*cf.* Matsuura, 1929) showed that five factors are involved in flower colour, thus :—

C	orange.
CG	yellow.
CF	flesh colour.
CR	red.
CRB	magenta.
c	white.

Ikeno was able to identify phenotypically three types of white. White (1) is free from all pigment, and when crossed to orange gives in the F_2, 3 orange : 1 white. White (2) has a few magenta spots on the petals or filaments, and when crossed to orange produces in the F_2, 9 magenta : 3 orange : 4 white. Pseudo-white (3) has reddish pigment in the stem and leaves, and purple spots at the base of the white petals. Pseudo-white **(Ps)C** × white (1) gives an orange F_1 and a ratio of 9 orange : 3 pseudo-white : 4 white in the F_2. Pseudo-white is **PsPsCC**. The heterozygote **PspsCC** does not inhibit the orange of **C**. This is an interesting case of incomplete epistacy, and shows the effect of balance between factors on the character expression.

In *Primula sinensis* (de Winton and Haldane, 1933) the following genes have been found to affect flower colour :—

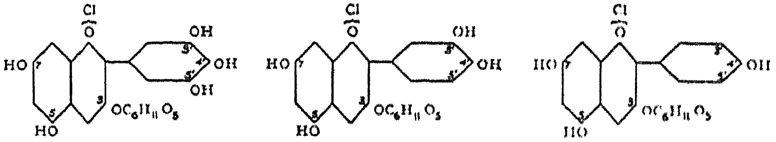
VKBR	magenta.
VKBr	blue.
VKbR	red.
VKbr	slaty.
VkBR	pale coral pink

VkBr	nearly white.
VkbR	coral pink.
Vkbr	pale coral pink.
v	all constitutions almost white, but some may be distinguished by chemical tests.

VK produces an anthocyanin, malvidin-3-monoglucoside, **B** produces a flavone which acts as a co-pigment and **R** may produce more acidity in the cell sap than **r**, or **r** may change the anthocyanin molecule.

Reference should be made to Matsuura (1933) who lists many other example of complex interaction of genes which control diverse characters in different species. The following species are to be recommended as striking examples of interaction—*Pharbitis Nil* (Imai, 1931*a*); *Portulaca grandiflora* (Yasui and Ikeno (see Matsuura, 1929)); *Linum usitatissimum* (Tammes, 1922, etc., Kappert, 1925*a*); *Lupinus angustifolius* (Hallquist, 1921); *Pisum sativum* (Winge, 1936).

Genetics of Plant Pigments. Onslow (1932, 1935), Willstätter, Karrer, Robinson and their collaborators have submitted plant pigments to chemical analysis. As a result of work on genetically known varieties there appears to be a regularity in the relation of chemical change and gene substitution. Scott-Moncrieff (1936) summarises the work on the chemistry of genetic material while Wit (1937) adds further evidence from *Aster*. The most important sap pigments for the production of coloured flowers are anthoxanthins—flavones and flavonols, and anthocyanins and their glucosides. Anthoxanthin production influences (*a*) the background colour—ivory (apigenin) to yellow (apigenin and luteolin); (*b*) the colour produced by anthocyanins—co-pigment effect (apigenin)—a blueing effect; (*c*) the degree of anthocyanin pigmentation by



Delphinidin 3-monoside

Cyanidin 3-monoside (Chrysanthemin)

Pelargonidin 3-monoside (Callistephin)

FIG. 10. Anthocyanin pigments.

TABLE 4.

(*Scott-Moncrieff*, 1936)

The biochemistry of flower-colour variation.

	Varieties		
	Dominant	Recessive	Factor
I. Yellow plastid production			
Cheiranthus Cheiri	Yellow	Lemon	**Y**
	Brown	Purple	
II. Yellow anthoxanthin production			
Antirrhinum majus	Yellow	White	**Y**
	Bronze	Rose doré	
Primula acaulis	Yellow	Ivory or white	**Y**
Dahlia variabilis	Yellow	White	**Y**
	Apricot	Magenta	
	Scarlet	Purple	
III. Ivory anthoxanthin co-pigment production			
Primula sinensis	Magenta	Red	**B**
Primula acaulis	Blue	Slaty	**W**
Dahlia variabilis	Bluish magenta	Rosy magenta	**I**
IV General anthocyanin production			
Primula acaulis	Magenta	Ivory or yellow	**B**
Dahlia variabilis	Magenta	Ivory	**A**
	Scarlet	Yellow	**B**
Antirrhinum majus	Magenta or red	Ivory	**L**
Cheiranthus Cheiri	Brown	Yellow	**(CR)**
	Purple	Lemon	
V. Specific anthocyanin production			
Primula sinensis	Orange	Coral	**Dz**
	Bright magenta	Magenta	
Papaver Rhoeas	Crimson-scarlet	Crimson-magenta	**T**
	Scarlet	Pink or salmon	
	Rose-crimson flushed	Pink	**F**
	Scarlet	Pink or salmon	
VI. Oxidation of anthocyanin aglycone	*Cyanidin*	*Pelargonidin*	
Antirrhinum majus (3-rhamnoglucosides)	Magenta	Red	**B**
Papaver Rhoeas (3-biosides)	Pink or crimson	Salmon	**E**
Cheiranthus Cheiri (3–5-dimonosides)	Purple	Pink	**P**
Dahlia variabilis (3–5-dimonosides)	Rosy-purple	Purple	General factorial balance
VII. Oxidation and methylation of anthocyanin	*Malvidin*	*Pelargonidin*	
Primula sinensis (3-monosides)	Red	Coral	**K**
Pelargonium zonale (3–5-dimonosides)	Pink	Salmon	**X**
	Peonidin	*Pelargonidin*	
Pharbitis nil	Purple	Red	$\mathbf{M}_g$
VIII. Local change in *p*H			
Primula sinensis	Magenta	Blue	**R**
Primula acaulis	Red	Slaty	**S**
Papaver Rhoeas	Scarlet	Claret	**P**
	Pink	Mauve	

competing for the common source from which both anthoxanthins and anthocyanins are manufactured.

The anthocyanidins are of three basic types pelargonidins, cyanidins and delphinidins, differing from one another only by hydroxyl groups at 3′ and 5′ on the side phenyl ring. Fig. 10 gives the formulæ of the glucosides of these types as chlorides—the most easily isolated form. The remaining anthocyanidins are derived from these by methylation, oxidation or both at 3′, 5′, and 7′. The anthocyanins in nature arise from anthocyanidins by the replacement of an H by a hexose or biose or pentose group at 3′ or 5′. Table 4 from Scott-Moncrieff classifies the chemical changes in relation to the gene changes. It will be seen that there is a fairly consistent relationship. In *Aster*, Wit finds a gene **M** which produces the sugar molecules at 3′ and 5′ of all genotypes, whereas the allelomorph **m** removes that at position 5′. A multiple allelomorphic series **R**, **r′**, **r** controls the number of OH groups—**R** produces OH at 3′ . 4′ . 5′; **r′** produces OH at 3′ . 4′ and **r** produces OH only at 4′—hence the types delphinidin, cyanidin and pelargonidin are interchanged by substitution in one allelomorphic series.

Intensification and inhibition of the anthocyanin production both throughout the plant and in parts of the flower may be influenced by genes. In addition, plastid pigments such as xanthophyll and carotin influence the final appearance. Co-pigmentation, oxidation, demethylation and increase in *p*H all tend to make the pigmentation due to anthocyanins more blue-toned.

Wit's analysis of the genetics and chemistry of the China Aster indicates the type of relation generally encountered. The gene **W** is a basic gene for the formation of chromogen necessary for general anthocyanin production. The allelomorph $\mathbf{w^d}$ only allows dilute colours to be produced and **w** prohibits anthocyanin production. The gene **M** determines the number of sugar molecules which are attached to the anthocyanidin molecule—two at positions 3′ and 5′. The allelomorph **m** prevents the sugar molecule at position 5′. The allelomorphs **R**, **r′** and **r** determine the number of OH groups at 3′, 4′ and 5′—**R** gives three OH groups, **r′** cuts out that at position 5′ while **r** cuts out both OH groups at 3′ and 5′. Thus the three basic types delphinidin, cyanidin and pelargonidin are controlled by one allelomorphic series. The allelomorphs **I** and **i** also influence the degree of oxidation of the pigment. The constitution **RI** gives delphinidin; **ri** gives pelargonidin. The presence of **I** and **r** add cyanidin to pelargonidin and **I** with **r′** gives a mixture of delphinidin and cyanidin. Other combinations give mixtures of varying composition. The stability of the pigment (viz., in sunlight) depends on **S**. **Pa** increases and the allelomorph decreases the amount of pigment present. The formulæ for the several colours in so far as they have been worked out are ·

TABLE 5

		WRPA	$\mathbf{Wr_1PA}$	**WrPA**
M	IS	violet blue	purple	carmine
	Is	violet	violet purple	deep carmine.
	iS	blue	lilac	deep pink.
	is	—	lilac purple	salmon pink.
m	IS	fading violet	fading purple	scarlet pink.
	Is	brown violet	brown purple	scarlet.
	iS	slaty blue	slaty purple	salmon pink.
	is	—	—	red.
		$\mathbf{w^dRPA}$	$\mathbf{w^dr_1PA}$	$\mathbf{w^drPA}$
M	IS	dilute blue	dilute lilac	dilute pink.
	iS	dilute purple	—	dilute shell-pink
m	iS	dilute slaty	—	dilute salmon.
		=wRPA	$\mathbf{wr_1PA}$	**wrPA**
		no colour.	no colour	no colour.

Overbeek (1935) has shown that the dwarf race of maize, due to the gene **na**, reacts to auxin less than normal and destroys more auxin than normal maize plants. The catalase activity of **nana** is 15–19 as compared with 10 in normal. Much experimentation is at present in progress connecting gene action and physiological phenomena.

Transplantation Experiments. Ephrussi, Clancy and Beadle (1936), Ephrussi and Beadle (1937), Beadle (1937) found by transplanting imaginal discs of an eye from a *Drosophila* larva of one genetic constitution to a larva of another constitution, that the implant may have an eye colour which does not correspond to its own genetic constitution. Thus vermilion disc transplanted to wild type gives wild type eye; vermilion disc transplanted to cinnabar eye host gives cinnabar. From these and other results it is postulated that three diffusible substances are involved in the colour-development of wild type eye. Cinnabar is deficient in one of these substances, $\mathbf{cn}^{+}$, and vermilion is deficient in $\mathbf{v}^{+}$ and $\mathbf{cn}^{+}$ while claret eye genotypes are deficient in $\mathbf{ca}^{+}$ substance. By studying many transplants the authors were able to postulate that a chain reaction—$\mathbf{ca}^{+}$ substance — $\mathbf{v}^{+}$ substance — $\mathbf{cn}^{+}$ substance — produces the three substances in a sequential order. The potentiality of one eye colour gene to approach the wild type gene in expression depends on whether **ca**, or **ca**, **v** or **cav** and **cn** are present in the discs. Fat bodies are concerned with the production of $\mathbf{v}^{+}$ and the Malphigian tubes of certain genotypes contain both $\mathbf{v}^{+}$ and $\mathbf{cn}^{+}$ substances. By inter-transplanting in four *Drosophila* species, Howland, Clancy and Sonnenblick (1937) showed that the vermilion genes in these species gave the same reactions as found within *Drosophila melanogaster*.

No controversy, but considerable loose thinking sometimes prevails on the nature of the relationship of gene action and interaction. A geneticist would not agree to the view that a phenotypic expression results directly from a gene. The new data from pigments illustrates the complicated nature of the relationship between gene and character. Competition for basic substances from which to manufacture specific colour pigments, and dependance of one gene's action on that of another are two of the many possible interactions. The complete ignorance of how the gene starts reactions necessitates mental caution in the use of the mnemonic terminology of genetics.

The terms dominant, recessive, epistatic, hypostatic, complementary, polymeric, duplicate (see p. 210), pleiotropic, lethal, sub-lethal and others are useful for purposes of description of the phenotypic effects and actions of the factors. It should be emphasised, however, that the nature of the factor itself is not designated by these terms. Further, there is an almost continuous series grading from one type of inheritance to that of another. For example, two factors together may give a 15 : 1 ratio or a 9 : 3 : 3 : 1 ratio or a 9 : 3 : 4 ratio or a 9 : 7 ratio or a 12 : 3 : 1 ratio.

In the first case each factor is completely dominant over the recessive allelomorph, and the phenotypic effect of both factor actions is similar. In the second case the expression of the actions of the two factors is different. In the remaining cases there are varying degrees of expression dependent on the ability of the factors to determine characters along or in conjunction with the complementary factor. These ratios depend on (1) our ability to separate one class of plants from another, *e.g.*, Blakeslee (1921*b*) was able to transform a 9 : 7 ratio into a 9 : 3 : 4 ratio by treating the young inflorescences of *Rudbeckia* with caustic potash, (2) the relative dominance of the factors over their allelomorphs, and (3) the genetic background of all the factors to the one considered. The character expression of a factor **A** may or may not be distinguishable from that of **a** unless certain other factors are present.

In the complex construction of a plant there will be many genes with wide and diverse effects. Some of these will be discussed under inheritance in pollen, dimorphism, incompatibility, lethal factors, xenia.

Inheritance of Pollen Characters. Various authors have considered the reasons for the deficiencies of the recessives in the maize examples quoted on p. 19. A percentage of 23·9% in place of 25% in the F_2 while 49·5% in place of 50% in the genetic output were found in the segregations of the recessive waxy in maize. All authors agree in suggesting that the growth in the style of the pollen tubes carrying the factor for waxy and for non-waxy respectively, is different. Brink (1924, 1925), and Brink and McGillivray (1924), showed that the cross, waxy × heterozygous non-waxy gave a lower proportion of waxy endosperms than the reciprocal cross. They have also shown by desiccation and other methods that the pollen tubes containing non-waxy and waxy exhibit different physiological reactions. Brink (1929*a*) finds that the extracts of waxy pollen tubes have less diastatic activity than extracts of non-waxy pollen tubes.

The styles of maize show a gradation in size from the top to the bottom of the ear. Brink and Burnham (1927) found that the upper and lower halves of the ear, when pollinated by pollen from a **Wxwx** plant, gave the same percentage of waxy endosperm. They were therefore led to the conclusion that in the early stages the two types of pollen grew at different rates, but in later stages at the same rate. The style contains sugars but the pollen contains starch or a starch-like carbohydrate, and the two types of pollen differ in the rate at which their extracts hydrolyse starch. This suggests that in the early stages the pollen tubes containing the non-waxy factor **Wx** differ in their physiological reactions from those containing the waxy factor **wx**, and that this is reflected in their growth rate. When all the starch reserve in the pollen is used up, both types of pollen tubes will absorb sugars from the style, and consequently the rates of growth at the later stages will not be affected by the difference in diastatic activity.

Mangelsdorf and Jones (1926) pointed out that in Kempton's data (1919) certain F_1 plants of maize, when selfed, gave the expected proportion of waxy : non-waxy progeny, but that others gave lower proportions of waxy than was expected. If plants which give the normal ratio are designated as N plants, and those which give a lower proportion of waxy as L plants, the following crosses can be made : L × N, L × L, N × L and N × N. Kempton's results showed that L × N and N × N have 25·1% and 25·4% of waxy grains respectively, but N × L and L × L gave 22·9% and 22·6% respectively when the expected in every case was 25%.

Thus, when N plants were used as male parents, the progeny gave results close to theoretical expectation, but when L plants were used as males the progeny gave 22·6% of waxy ; a deviation from expectation of 5·8 times the probable error. It is presumed by the authors, therefore, that an accessory factor is sometimes coupled to waxy, which reduces the number of waxy-carrying pollen tubes affecting fertilisation. This had also been suggested by Brink and McGillivray (1924).

Mangelsdorf (1931) passed sugary and starchy pollen through sieves of 0·088–0·062 mm. apertures. When the different fractions were used for pollination it was seen that the sugary and starchy characters were associated with size of pollen. Only 25% sugary plants were produced from the smallest fraction whereas 93% resulted from the largest fraction.

Mangelsdorf and Jones (1926) found that the factor $\mathbf{de}^1$ causing defective seeds in maize was linked to **Ga**, a factor which speeds up pollen tube growth. The result of another series of experiments relating to plants with sugary endosperm have been brought into line with those of **de**^{1} by East and Hayes (1911), Jones (1924) and Emerson (1925). Owens (1902) found that the F_2 of the cross "Rice pop" × sugary always had too few grains with sugary endosperm; generally there were 16·2% instead of 25%. Control crosses showed that when the homozygous dominant **Su Su** (cornaceous) was crossed with the heterozygote **Susu** there was a large excess of **SuSu** plants in the progeny. When the female parent was **susu** there was no marked deviation from the expected ratios. Jones (1924) concluded that there was apparently an interaction between the pollen tubes and the stylar tissue such that pollen tubes carrying the dominant factor **Su** were more able to accomplish fertilisation than the pollen carrying its recessive allelomorph **su**. This only occurs in a sporophyte which also has the dominant factor present either in the homozygous or heterozygous state.

Brink and Burnham (1927) showed that the sugary factor **su** might exert a differential action on **Wx** and **wx** pollen, leading to marked deficiencies in the waxy: non-waxy ratio. This occurs only when the pollen parent is **susuWxwx**, and not when doubly heterozygous **SusuWxwx**. To account for the different reactions between homozygous **susu** plants and heterozygous **Susu**, the authors suggested that **susu** plants exerted a cytoplasmic influence on the pollen tubes, retarding the growth of **wx** pollen tubes as compared with **Wx**. It is interesting to note that Brink does not find differences in diastatic activity between **Su** and **su** pollen as he did between **Wx** and **wx**.

Mangelsdorf and Jones (1926) show that **Ga**, **Su** and **de**^{1} are linked together and that the peculiar behaviour of **Su** and **de**^{1} is due primarily to their relationship to **Ga**. They therefore brought into line the factor for defective seeds **de**^{1} and **Su** which also gives a reduced number of recessives 19·8%.

Brieger, Tidbury and Tseng (1938) have shown by scoring the phenotypes in each quarter of the ear that **Ga**$_2$ and **ga**$_2$ carrying pollen tubes grow at different rates, while a new gene **ga**$_3$ linked with **C**, **sh**, **wx**, also shows a reduced rate of pollen tube growth and may be the cause of the aberrant ratios of **wx**.

Certation. Heribert-Nilsson (1920) found that reciprocal crosses in *Œnothera Lamarckiana* between red-nerved plants **Rr** and non-red-nerved plants **rr** gave different proportions of the two types, **Rr** × **rr** gave a ratio of 1 : 1 (181 : 174) as expected, while an excess of red-nerved plants appeared in the reciprocal cross, 254 : 93. He suggested that the pollen tubes carrying **R** grew faster than those carrying **r**. This competition in growth of the pollen tubes of different genetic type he named *certation*. He also found that the difference in rates of growth of the two types was influenced by external environmental factors such as temperature. Davis (1926) using F_1 plants from the cross *Œnothera Lamarckiana* × *O. Nanella brevistylis*, which are heterozygous for the factor for red-nerved **R**, decapitated the style at various intervals of time after pollination. He found a ratio of 1 **Rr** : 5 **rr** when the styles were cut off 23 hours after pollination and 1 **Rr** : 2·8 **rr** after 27 hours. Davis shows that the pollen of the mutant *Œnothera brevistylis* is slower in growth than that of *O. Lamarckiana*, while Hiorth (1916) reports several crosses in the genus where differences in pollen tube growth are found (see p. 270). Sirks (1926*b*) obtained similar differences in ratios of *Datura*, involving the characters purple-white, armed inermis.

In *Melandrium*, Correns (1918, 1921) found that pollination with few pollen grains gave 50% of males in the progeny, but with much pollen the average percentage was 35% males. Certation between the male and female determining pollen tubes appears to be the cause of this difference. Where much pollen was applied, the female determining pollen tubes achieved fertilisation more often than the male determining pollen tubes.

This difference in growth rate was confirmed by Correns by another method. He found that the seed from the upper or stylar half of the ovary gave 32% males while the lower half gave 45% males. This indicates that the ovules nearest to the base of the style were fertilised by the faster growing female determining pollen tubes, thus forcing the male determiners to travel further down the ovary to reach an unfertilised ovule. Further, by cutting off the styles at a definite time after pollination, Correns showed that more females were obtained in the progeny. This again supports the view that the nucleus of the female determining pollen grain reaches the ovule more quickly than that of the male determining grain.

If the pollen grains of *Melandrium* are either exposed to alcohol vapour, or allowed to age by keeping, there is a larger mortality of the female determining grains than of the male determiners. Similar results were found by Correns in *Rumex acetosa*, while a considerable number of examples of certation are to be found among the later described aneuploids (see p. 243).

Nilsson Ehle (1911*b*) in Wheat, Bateson and Sutton (1919) in Begonia, Saunders (1928*a*), Frost (1915), Snow (1924, 1925), Waddington (1929) and Philp and Huskins (1931) in Stocks, have found further examples of certation.

Dimorphism of Pollen. The contents of the pollen grains in several species differ in a genetical manner. For example, Renner (1919*a*,*b*) showed that the shape of the starch in the different pollen grains of some *Œnothera* species was different. *Œnothera curvivelutina* (*Lamarckiana* × *muricata*) has two types, one (*Lamarckiana*) (see p. 270) having large spindle-shaped starch grains and the other (*muricata*) with smaller, thicker, blunt-ended starch grains.

Strasburger (1910) found that the pollen grains of *Elodea* remained together in tetrads so that he was able to obtain the four pollen grains which arise from the division of one pollen mother-cell. The male plant of *Elodea* is dimorphic in respect of the sex chromosomes (Santos, 1924) and produces two kinds of pollen—a male determining and a female determining. By pollinating a stigma with one tetrad, Strasburger showed that the progeny segregated into two males and two females and that never more than $n/2$ females or $n/2$ males resulted from n tetrads. He therefore showed that segregation of sex determiners occurred during the formation of the pollen grains.

Santos (1924) found that there were two larger and two smaller pollen grains to each tetrad which corresponded to the male and female determining pollen grains of *Elodea* respectively.

Bimodal curves for size of pollen grains have been found in *Cannabis sativa* (Sinoto, 1930), *Melandrium* (Tischler, 1925), and *Rumex acetosella* (Sinoto, 1930) among others (see Sinoto, 1930). These plants have sex chromosomes and the authors correlate the two sizes of pollen grains with the fact that segregation of sex determiners by means of sex chromosomes takes place during the reduction division in these plants.

SELF-INCOMPATIBILITY AND CROSS-INCOMPATIBILITY

De Vries (1906) was the first to find intra-sterile inter-fertile groups of plants within a species—*Linaria vulgaris.* Among other species where similar intra-sterile inter-fertile groups are found are *Antirrhinum hispanicum,* Baur (1919), Brieger (1935), *Petunia violacea,* Shull (1924), Wergen (1936), *Capsella Bursa-pastoris,* Shull (1926) and Kikuchi (1926, 1929), *Reseda odorata,* Compton (1912, 1913), *Brassica oleracea* var. *capitata,* Detjen (1927) and Kakizaki (1930), *Veronica syriaca,* Filzer (1926) and Lehmann (1926), *Verbascum phœniceum,* Sirks (1926*a*), *Cardamine pratensis,* Correns (1913), Baur (1924) and Beatus (1929, 1931), *Nicotiana,* spp. East and his co-workers (1917–1935), *Prunus,* spp. and *Pyrus Malus,* Crane and Lawrence (1923–1932), Crane and Brown (1937), Sears (1937).

In the case of incompatible pollinations it has been found that either the pollen tube grows so slowly that it is unable to reach the ovule before the flower withers, or the growth of the pollen tube is completely inhibited.

Through the independent work of East and Mangelsdorf (1926), Lehmann (1926), and Sirks (1926*a*) on species of *Nicotiana, Veronica* and *Verbascum* respectively, the oppositional factor hypothesis for incompatibility was placed on a sound basis. The hypothesis had been suggested by Prell (1921) in a paper surveying the work of others. East and his co-workers (1925–1929) independently put forward the same hypothesis, and credit must be given them for providing extensive evidence of the validity of the oppositional factor hypothesis.

Oppositional Factor Hypothesis. The work of East and Park (1917) on crosses between *Nicotiana Tabacum* and *N. Sanderæ* showed that there were three intra-sterile, inter-fertile groups x, y and z. All plants in each group were found to be self-sterile and intra-sterile, but plants of different groups were inter-fertile. A cross between group x and group y gave an F_1, consisting of equal numbers of plants belonging to groups y and z, while the reciprocal cross $y \times x$ gave equal numbers of z and x plants. It is significant that one of the classes in each F_1 corresponds to that of the male parent. East and Mangelsdorf (1926) put forward the suggestion that this behaviour is governed by a multiple allelomorphic series of incompatibility factors, and that pollen tubes carrying an incompatibility factor will not function properly in stylar tissue having the same incompatibility factor.

The assumption is made that plants of group *x* have the factors S_1S_3, plants of group *y* have S_1S_2, and plants of group *z* have S_2S_3. In the cross *x* × *y*, ($S_1S_3 \times S_1S_2$) only S_2 pollen tubes are normally able to bring about fertilisation. Consequently this cross produces *z* (S_2S_3) and *y* (S_1S_2) groups in equal numbers. In the reciprocal cross *y* × *x*, ($S_1S_2 \times S_1S_3$) only S pollen tubes function, therefore the progeny consists of *x* (S_1S_3) and *z* (S_2S_3) groups in equal numbers (see Fig. 11).

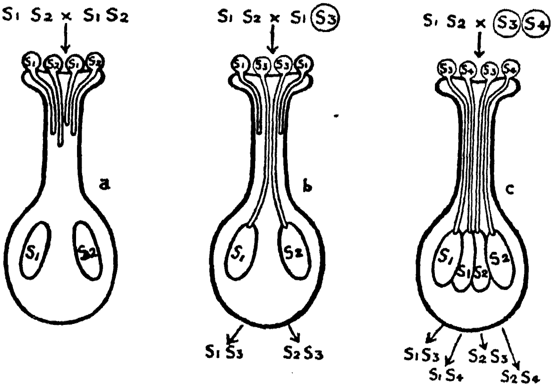


FIG. 11. Compatible and incompatible pollinations. (Crane and Lawrence, 1929.)

By pollinating in the bud stage it is sometimes possible to obtain seed from normally incompatible pollinations. This may be explained in either of two ways. Either the inhibition of pollen tube growth is less intense at the bud stage, or the greater length of time between pollination and the withering of the style allows the slow growing pollen tubes to reach the ovules. Four plants of the constitution y (S_1S_2) were selfed in this manner and gave progeny of 14 S_1S_1 : 81 S_1S_2 : 38 S_2S_2 plants. The homozygous plants S_1S_1 and S_2S_2 when selfed in the bud bred true, and when normally pollinated with pollen from S_1S_2 plants gave only S_1S_2 plants.

The cross $S_1S_2 \times S_2S_2$ produces offspring of the S_1S_2 class. This class is incompatible when used as a female in crosses with either parent, but may be used successfully as male parent with either. In each case it gives progeny of the S_1S_2 type due to the functioning of pollen tubes carrying unlike factors. Similarly the cross $S_1S_1 \times S_1S_2$ will be fertile, giving S_1S_2 progeny, while the reciprocal cross will be incompatible.

Later Brieger and Mangelsdorf (1926) found that the multiple allelomorphs S_1, S_2 and S_3 were linked with a factor C which controlled the development of colour in the flower, seed, and stem. The cross-over percentage in one plant, estimated from its progeny of 576 plants, was 24·5 ± 1·2% on the male side and 18·2 ± 1·1% on the female side. In another plant the cross-over percentage was 16·2% on the male side and 14·5% on the female side, estimated from a progeny of 220 plants.

Fifteen incompatibility factors in this allelomorphic series have so far been found, and hence an increased number of inter-fertile intra-sterile groups. The different factors have noticeably different degrees of reaction. For example, S_3 in the homozygous condition tends to be lethal, causing the plants to be dwarf with wrinkled leaves and abnormal growth and to be practically male sterile (East, 1930).

Homozygotes of some factors may be obtained with comparative ease, whereas other factors are difficult to obtain in the homozygous condition.

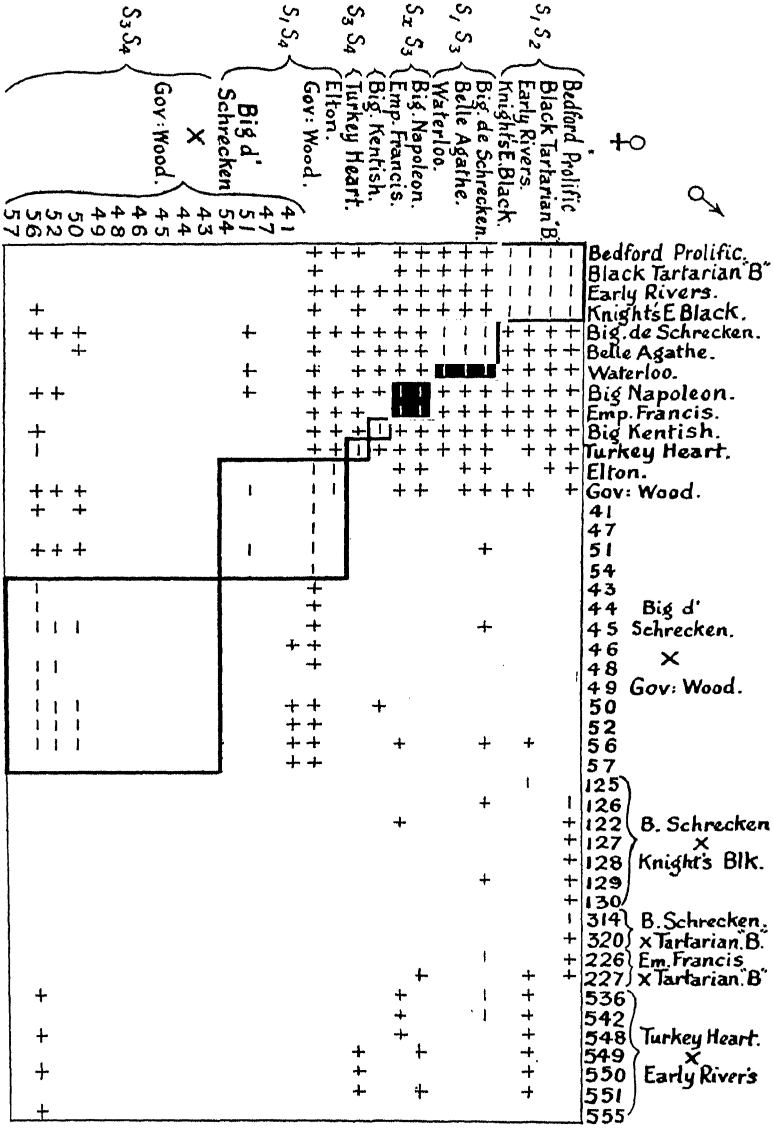
East and Yarnell (1929) and East (1932) have found that there is a fertility factor S_f, which is a member of this allelomorphic series. Plants having the constitution S_fS_x, where S_x is any other factor of the series, will be self-fertile, and on selfing will only give self-fertiles of the constitution S_fS_f and S_fS_x.

S_fS_x plants may be crossed with any self incompatible plant of the species and consequently self-incompatibles together with self-compatibles will appear in the progeny. Anderson and de Winton (1931) found another allelomorph S_F which is able to inhibit the pollen tubes carrying the S_1 factor.

Filzer (1926) and Lehmann (1926) independently put forward a similar hypothesis to explain the data in *Veronica syriaca*. All plants are self-incompatible. Seventeen individuals were crossed in all possible ways, and were found to fall into four intra-sterile, inter-

TABLE 6

Compatible and Incompatible Crosses in Cherries (*Crane and Lawrence*, 1931).



S_3S_4										S_1S_4						S_3S_4	S_xS_3			S_1S_3			S_1S_2				♀	
Gov: Wood. ×										Big d' Schrecken				Gov: Wood.	Elton.	Turkey Heart.	Big. Kentish.	Emp. Francis.	Big. Napoleon.	Waterloo.	Belle Agathe.	Big. de Schrecken.	Knights E. Black.	Early Rivers.	Black Tartarian "B".	Bedford Prolific.	♂	
57	56	52	50	49	48	46	45	44	43	54	51	47	41															
														+	+	+		+	+	+	+	+	−	−	−	−	Bedford Prolific.	
														+				+	+	+	+	+	−	−	−	−	Black Tartarian "B"	
														+	+	+	+	+	+	+	+	+	−	−	−	−	Early Rivers.	
	+													+		+		+	+	+	+	+	−	−	−	−	Knights E Black.	
	+	+	+								+			+	+	+	+	+	+	−	−	−	+	+	+	+	Big. de Schrecken.	
			+											+		+	+	+	+	−	−	−	+	+	+	+	Belle Agathe.	
											+			+		+	+	+	+	■	■	■	+	+	+	+	Waterloo.	
	+	+									+			+	+	+	+	■	■	+	+	+	+	+	+	+	Big Napoleon.	
														+	+	+		■	■	+	+	+	+	+	+	+	Emp. Francis.	
	+													+	+	+	−	+	+	+	+	+	+	+	+	+	Big Kentish.	
	−													+	+	−	+	+	+	+	+	+		+	+	+	Turkey Heart.	
														−	−			+	+		+	+			+	+	Elton.	
	+	+	+								−			−	−			+	+		+	+	+	+		+	Gov: Wood.	
	+		+											−													41	
														−													47	
	+	+	+								−			−								+					51	
														−													54	
	−													+													43	Big d' Schrecken. × Gov: Wood.
	−													+													44	
	−	−	−											+								+					45	
													+	+													46	
	−	−												+													48	
	−																										49	
	−	−	−										+	+			+										50	
	−	−	−										+	+													52	
	−	−	−										+	+				+				+		+			56	
													+	+													57	
																								−			125	B. Schrecken × Knight's Blk.
																						+				−	126	
																		+								+	122	
																										+	127	
																										+	128	
																						+				+	129	
																										+	130	
																										−	314	B. Schrecken. × Tartarian "B"
																										+	320	
																						−				+	226	Em. Francis × Tartarian "B"
																			+					+		+	227	
	+																	+				−		+			536	Turkey Heart. × Early Rivers
																		+				−		+			542	
	+																	+						+			548	
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	+																										555	

Since the above table was published, Crane and Lawrence have found that $S_x = S_5$ and Turkey Heart probably does not carry both S_3 and S_4.

fertile groups consisting of seven, five, three and two individuals respectively. Intercrossing plants of any two groups produced plants of two groups in equal numbers, except in one case, where all four groups were obtained. If the four groups A, B, C, D were determined by four factors S_1, S_2, S_3, S_4 (the authors, however, use the symbols $a,_1$ b_1, c_1, d_1) then A is S_1S_3, B is S_2S_4, C is S_1S_4, D is S_3S_4, and the cross A × B will give plants of all four groups, while every other type of cross will give two groups.

Crane and Lawrence (1923–1932) have shown that all varieties of sweet cherries are self-incompatible and fall into nine intra-sterile inter-fertile groups. Reciprocal crosses between varieties of one intra-sterile group are sterile. The authors point out that the results are amenable to East and Mangelsdorf's hypothesis of "incompatibility" factors. By intercrossing varieties of different groups it has been shown that some groups have a factor in common. For example, the cross Biggarreau de Schrecken of group 2 with Governor Wood of group 6 gave two intra-sterile inter-fertile groups in the progeny, one of which fails with the male parent, Governor Wood. Hence, it can be assumed that Big. de Schrecken is of the constitution S_1S_3 and Governor Wood S_1S_4. Similar results indicate that group 1 is S_1S_2, group 2 is S_1S_3, group 3 is S_3S_5, group 4 is S_2S_3 and group 6 is S_1S_4 (see Table 6).

In the sour cherries, which are tetraploid, and plums which are hexaploid, partially self-compatible varieties are known as well as self and cross incompatible varieties. In the plums complete self-compatibility is also found. The results of Crane and Lawrence afford strong evidence that a hypothesis similar to that of East and Mangelsdorf is applicable to these phenomena in these polyploid fruits, but that the nature of these plants increases the complexities of behaviour. When pollen tubes carrying S_1 will not grow down S_1S_2 styles it is difficult to say what the reaction of pollen tubes with $S_1S_1S_2$ factors will be in a style of the constitution $S_1S_1S_2S_2S_3S_3$, a situation which is possible in the hexaploid plums. Grades of self-incompatibility, together with a considerable proportion of one-way incompatibility, are to be expected in tetraploid and hexaploid species. For example, the hypothetical cross $S_1S_1S_2S_2 \times S_1S_1S_2S_3$ may be compatible as a result of the pollen bearing S_3 with one other factor, but the reciprocal cross may be expected to be incompatible.

Sirks applied the oppositional factor hypothesis to explain incompatibility in *Verbascum phœniceum,* but found one-way incompatibility to be frequent. Crane and Lawrence suggest that since the chromosome number of *V. phœniceum* is 32, it is possibly a tetraploid. If this is indeed the case the polyploid nature of the species is a sufficient explanation of the phenomenon.

Apples vary in their degree of self-compatibility, but only two varieties are possibly completely self-incompatible. Crane and Lawrence (1930*a*), and Darlington and Moffett (1930), showed that the apple was a secondary polyploid. Instead of containing 17 non-homologous chromosomes in the haploid set, the apple contains four sets of two homologous chromosomes and three sets of three homologous chromosomes. The primary basic chromosome number is presumably seven, *i.e.*, there are only seven different types of chromosome present in the haploid set, but all are repeated more than once (see p. 222). We therefore expect the apple to behave like a complex polyploid in its mode of inheritance. The self and cross incompatibility results appear to be of this nature.

TABLE 7

Showing Inverse Correlation between Chromosome Number and Complexity, and the Frequency of Incompatibility (after Crane, 1932).

	Number of varieties tested.	Percentage of varieties completely self-incompatible.	Percentage of varieties completely cross-incompatible.
Cherries ($2x = 16$) . .	40	100	70
Plums ($6x = 48$) . .	53	40	13·5
Apples			
Secondary diploid ($2n = (3 \times 6 + 4 \times 4)$).	42	4·8	4·8
Secondary triploid ($2n = (3 \times 6 + 4 \times 4)\frac{3}{2}$).	5	0	0

Kakizaki (1930) obtained some interesting results from experiments with the cabbage. Here there are two types of self-incompatible plants; one which gives only self-incompatible progeny, and the other which segregates into self-compatible and self-incompatible progeny in a ratio of 1 : 3. Self-compatibles always segregate again into two types in a ratio of 50% self-incompatible : 50% self-compatible. Certain matings between two self-compatible plants are reciprocally incompatible, and between self-compatible and self-incompatible plants some matings are compatible only when the former is the female parent and in other matings when the latter is the female.

These facts obviously cannot be explained by East and Mangelsdorf's hypothesis alone. Kakizaki suggests that besides the oppositional allelomorphic series of S factors there are sympathetic factors T_1 and T_2 which influence the pollen tube growth in the style. The S series is supposed to be epistatic over the T series, but T in double dose is more active than an S factor in single dose. For example, $S_1S_1T_1T_1$ would be self-incompatible, since S_1 is in equal dosage to T_1 and is epistatic over T_1. In $S_1S_2T_1T_1$, T_1 would cause the plant to be self-compatible. Some of the self-compatible plants would have the constitution $S_1S_3T_1T_1$ and would segregate on selfing into

1 $S_1S_1T_1T_1$ self incompatible
1 $S_3S_3T_1T_1$,, ,,
2 $S_1S_3T_1T_1$ self-compatible
or a ratio of 1 : 1.

Self-incompatible plants could be of the constitution $S_2S_3T_1T_2$ and would give a dihybrid ratio on selfing in the bud stage as in *Nicotiana*. Only four out of the sixteen possible matings of gametes would give self-compatible plants, *i.e.*, two $S_2S_3T_1T_1$ and two $S_2S_3T_2T_2$ and the ratio obtained on selfing such a self-incompatible plant would be four compatibles to twelve incompatibles or 1 : 3.

This interesting hypothesis of Kakizaki merits further investigation. Lawrence (1930), however, points out that *Brassica* has basic numbers of 8, 9 and 10, and that the evidence from the number of chromosomes in the Cruciferæ indicates that *Brassica* may be a secondary polyploid. We therefore suggest that Kakizaki's results may be the result of polysomic inheritance of incompatibility factors as Crane and Lawrence have already found in plums and apples.

Physiology of Pollen Tube Growth. That incompatibility is closely connected with pollen tube growth in the style, is supported by the histological studies of various workers. Jost (1907) finds that in *Lilium* the pollen tubes of self-incompatible plants grow so slowly that fertilisation is not achieved. Martin (1913) found that pollen tubes in self-pollinated red clover grew much more slowly than pollen tubes in a cross pollinated plant. Coe and Martin (1920), and Williams (1925), found that when red clover was pollinated in the bud stage it set more seed. Williams suggests that this fact may be correlated with the slow growth of its own pollen tubes.

In the apple Sansome finds that the pollen tubes descend inside each style as in *Primula sinensis.* Other investigators, among whom are Correns (1913) for *Cardamine pratensis,* Compton (1913) for *Reseda,* Moore (1917) for *Tradescantia,* Crane and Lawrence for cherries, plums and apples, East and Mangelsdorf for *Nicotiana,* Sirks for *Verbascum* and Gregor (unpub.) for *Lolium* and *Dactylis,* hold that the pollen tube growth in the style is the cause of compatibility or incompatibility of the matings in these plants.

Sears (1937) has made a histological study of incompatible pollinations in various species. He shows that the reaction to the pollen tube takes place on the stigma, in the style or in the ovule. To the first group belong *Brassica, Raphanus, Pelargonium* and *Secale.* Inhibition in the style is found in *Petunia violaceæ, Abutilon, Nicotiana, Linaria, Nemesia.* Degeneration of the ovules occurs in *Gasteria.*

Whether incompatible pollen tubes are inhibited in growth or whether compatible pollen is accelerated or whether both inhibition and acceleration may be present in these plants is as yet undecided. The success of pollination in the bud, of incompatible matings in *Nicotiana,* red clover and cabbage does not decide the matter since the development of inhibitory substances may be restricted to a certain period in stylar degeneration. End-season fertility, by which normally self-sterile plants may give some seeds late in the season of growth, has been reported in *Nicotiana,* East (1923) and Anderson (1924), and in *Lythrum,* Stout (1922, 1923). It has been used by Kakizaki (1930) to support the view that there is an inhibitory action which wanes at the end of the season. This hypothesis, however, is open to the objection that the flower does not wither so quickly at that time, therefore the slower growing tubes achieve fertilisation owing to the time factor alone.

Evidence obtained by Kakizaki, Crane, and Lawrence, however, suggests that both inhibition of incompatible and acceleration of compatible pollen tubes takes place. In a tetraploid, although $S_1S_1S_2S_2$ stylar tissue will not allow S_1S_1 pollen to fertilise the ovules, pollen tubes carrying S_1S_3 may be able to reach the ovules, due possibly to an acceleration of growth caused by the presence of S_3. Here again there may be the objection that the ability of such a pollen tube to grow may be due simply to the nullification by S_3 of the inhibitory action of S_1; the production of some inhibitory substance normally induced by S_1 may be stopped at the source by the presence of S_3, rather than as implied by Lawrence, to the production of both inhibitor and accelerator which interact with one another.

It should be mentioned, in passing, that the solution of the problem of incompatibility is of great importance to the fruit grower. It was well known, in an empirical manner, that certain fruit trees, if planted in isolation or in certain mixtures of varieties, were unproductive, and that certain other mixtures of varieties were productive. The scientific analysis has shown the cause of incompatibility and furnishes valuable information as to which trees will be compatible *inter se*.

All the above examples furnish evidence that the pollen grain carries genetic factors and that these genetic factors have been segregated one from another at the meiotic division which is undergone by the nucleus during the formation of the microspore from the microsporocyte.

Belling (1914) found that when he crossed two races of *Stizolobium* 50% of the pollen and eggs aborted, and Brink (1929*b*) found a similar behaviour in maize. A hypothesis was put forward that there were two pairs of allelomorphs **Aa Bb** and that the gametes with the constitutions **AB** and **ab** were non-viable. Belling and Brink, however, make the important suggestion that some interchange or translocation in the chromosomes may account for these cases. Later we shall see that the latter explanation is substantiated by related facts.

FUNGI

Heterothallism in the Fungi was first discovered by Blakeslee (1904) in certain species of the Mucorales. He showed that in these Fungi there were two strains morphologically similar but physiologically different. One strain must come into contact with the other before sexual reproduction could take place. Blakeslee differentiated the strains by the symbols + and – and for some considerable time they were regarded as sexually differentiated. However, the very considerable work on Fungi by Kniep, Gwynne-Vaughan, Cayley, Dodge and others indicates that heterothallism is a form of incompatibility analogous to that discussed in Angiosperms. Indeed the phenomenon of "aversion" (Cayley, 1931) bears the same relation to sexual differentiation as heterostylism and incompatibility. We shall therefore use the terms of incompatibility in place of those of sex determination in describing the phenomena.

Phycomycetes. Burgeff (1928) investigated the behaviour of various so-called mutant forms of *Phycomyces Blakesleeanus* when intercrossed and when crossed with the original type. The different forms were piloboloides (**ba**), gracilis (**gra**), mucoroides (**muc**), arbusculus (**arb**) and pallens (**pal**). Each type appears to be controlled by a single factor and all except mucoroides are recessive to the normal form. Various combinations of these factors with the plus and minus incompatibility factors were made.

Where two or more pairs of factors were segregating, it was possible to determine whether or not both factors segregated at the first or second division.

In the case of the heterozygous zygotes (**Arb arb,** + –) it was found that 50% (called tetrakrats) gave four different haploid derivatives having the respective constitutions **Arb** +, **Arb** –, **arb** +, **arb** –, and 50% (called dikrats) gave only two types of derivatives; either **Arb** + and **arb** – or **Arb** – and **arb** +. If the segregation of both pairs of factors takes place at the first division, only two haploid types are expected from each zygote—either **Arb** + and **arb** – or **Arb** – and **arb** +. If the two factors segregate independently the two types should occur with equal frequency. The fact that 50% of the zygotes produce four types of haploids as a result of meiosis indicates that one or both of the factor pairs must segregate at the second division.

Ascomycetes. Shear and Dodge (1927) and Dodge (1927, 1928) isolated the eight spores from a single ascus of the heterothallic

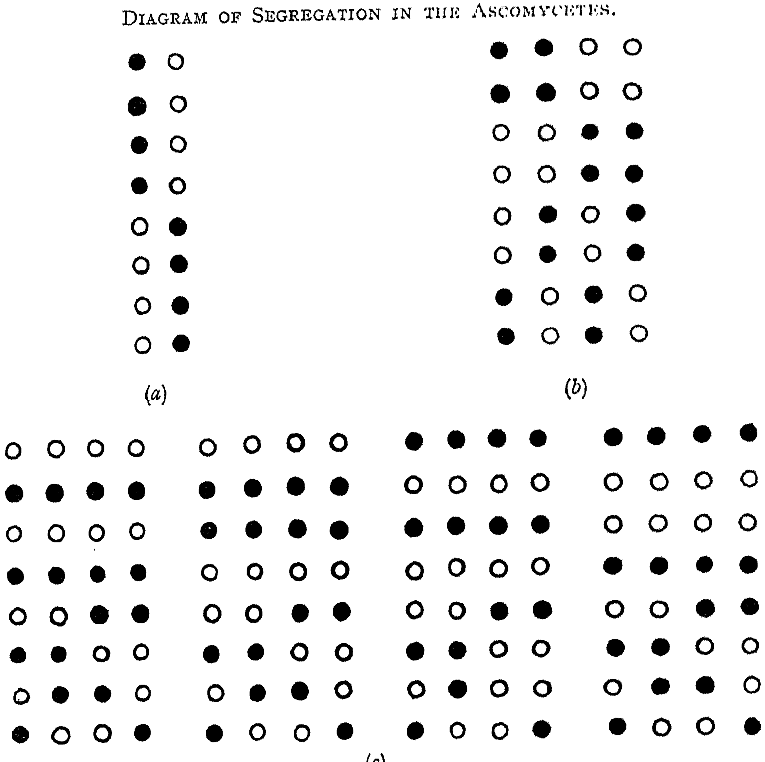

FIG. 12. Scheme of the position of spores in the ascus of *Neurospora sitophila*, when (*a*) the first division is reductional; (*b*) the second division is reductional; and (*c*) the third division is reductional. (After Dodge, 1927.)

Neurospora crassa and found that four were of one group (+ or −) and four were of the alternative group. This indicates that segregation of the incompatibility factors takes place in the formation of the ascospores, but it does not indicate at which of the three divisions the segregation occurs.

Dodge made a cytological investigation of *N. sitophila* and found that the spindle axes of divisions 1 and 2 were in a longitudinal direction with regard to the length of the ascus, while that of division 3 was transverse.

Dodge considered the end products of segregation of the factors when it occurred at the first, second or third divisions. The diagram (Fig. 12) shows the different arrangements of spores in the ascus with the three possible types of segregation.

Wilcox (1928) isolated the eight spores which lie in a row in the ascus of *N. sitophila* and identified them according to their position in the row. The plus and minus spores alternated in pairs in each half of the ascus. Here, therefore, the incompatibility factors must have segregated at the second division of the ascus nucleus.

N. tetrasperma (Shear and Dodge) is homothallic and normally forms four large spores in place of eight small spores. Sometimes two small spores take the place of one large spore. The resulting mycelia from these small spores are heterothallic. About half of the small spore cultures were plus and half were minus strains. The normal large spores were homothallic through containing both plus and minus factors. Dodge (1928) believes that the incompatibility factors probably segregate at the second division in *N. tetrasperma.*

Cayley (1931) investigated the phenomenon of aversion in *Diaporthe perniciosa.* She found that intra-perithecial aversion in which mycelia derived from the spores of one perithecium refused to mix, could be explained by the assumption of two or more pairs of factors which segregated independently of each other. The results seem to indicate that segregation either takes place at the first or second division of the ascus. Drayton (1934) and Ames (1934) have shown that incompatibility factors are present in the hermaphrodites *Sclerotina Gladiolii,* and *Pleurage anserina.*

Basidiomycetes. Kniep (1922) found four different strains in *Schizophyllum commune* and *Aleurodiscus polygonius.* He assumes therefore that " sex " is determined by two pairs of factors **Aa Bb** which segregate in the formation of the basidiospore. Meiosis occurs in the basidium immediately after fertilisation which takes place by the fusion of the two nuclei of the young basidium. The only possible zygote is of the constitution **AaBb.** The spores can be of the constitutions **AB, Ab, aB, ab,** if the pairs of factors **Aa** and **Bb** segregate independently as is supposed. The four strains will only fuse in such a manner that unlike factors attract and like factors repel one another. Hence fusion will take place between mycelia bearing **AB** and **ab**, or **Ab** and **aB**, but in no other way.

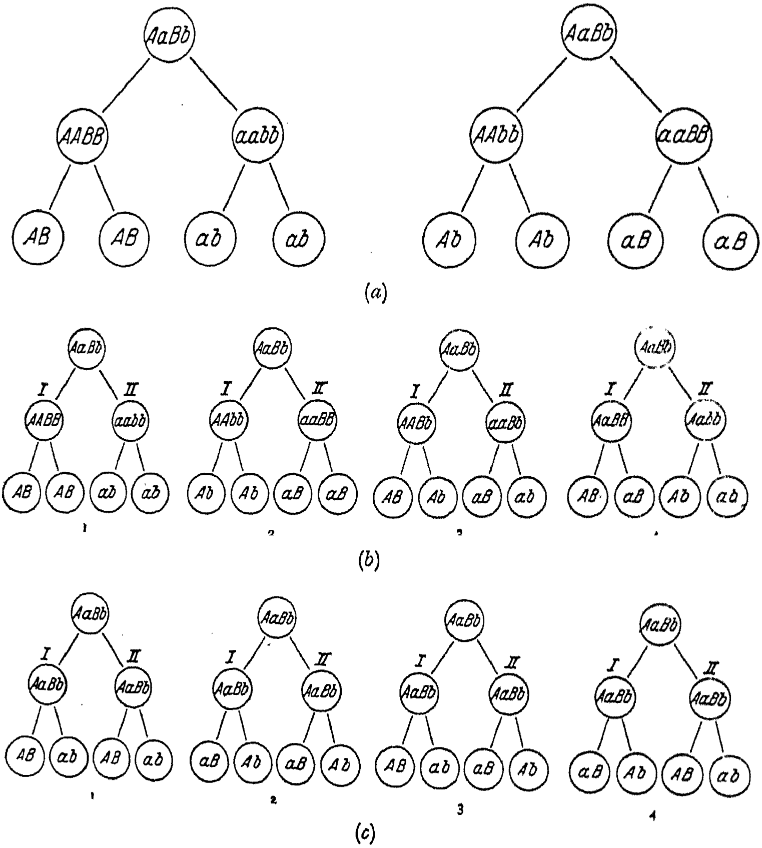

FIG. 13. Scheme of the segregation of two independent pairs of factors *Aa* and *Bb* (*a*), where the first division of meiosis is reductional; (*b*) where the second division is reductional; (*c*) where both factor pairs segregate at the first division (1) and (2), and where one factor pair segregates at the first and the other pair at the second (3) and (4). (Stern, 1928.)

In *Aleurodiscus*, Kniep found that a basidium gave rise to two types of spores—either **AB** and **ab**, or **Ab** and **aB**. No basidium produced all the combinations. This indicates that segregation takes place at the first division of meiosis (see diagram, Fig. 13). In *Coprinus lagopus* Hanna (1925) and Newton, D. E. (1926) find that there are three classes of basidia, (1) those which give all four possible combinations, (2) those which give two **AB** and two **ab**, and (3) those which give two **Ab** and two **aB**. Hanna therefore concludes that segregation of the incompatibility factors takes place at the second of the two divisions in this species.

Funke (1924) came to a similar conclusion with regard to *Hypholoma fasciculare, H. capriodes* and *Collybia velutipes*. Newton considers the results in *C. lagopus* to be best explained on two assumptions, (1) that the two incompatibility factors in the nucleus of each spore segregate independently, and (2) that in some basidia the segregation of both incompatibility factors takes place at the first division, and in the other basidia the segregation of one pair of factors takes place at the first division and the other pair at the second. A third possibility, as Hanna concludes, that both pairs of factors segregate at the second division, must not be neglected.

Newton also investigated *C. Rostrupianus* in which incompatibility was controlled by one pair of factors. By observing the behaviour of basidiospores, whose position in the basidium was known, she was able to show that segregation of the incompatibility factors sometimes took place at the first and sometimes at the second division of meiosis in this species. The first division will produce two cells while the second division of these two cells will produce four cells which are orientated at right angles to the first division spindle. Hence if segregation takes place at the second division one expects that sometimes the spores at opposite corners of the basidium will be similar in constitution (see Fig. 13).

Brunswik (1924) in *Coprinus curtus, C. deliquescens, C. ephemerus* and *C. fimetarius* also found more than two apparent sex forms, but suggested that in some cases the Fungi were potentially bisexual, and fusion was controlled by one or two pairs of self-incompatibility factors.

Brunswik analysed 93 tetrads of *C. fimetarius* (*lagopus*) with the following results :—

37 gave four different types of spores **AB, Ab, aB** and **ab**
29 ,, two ,, ,, ,, **AB** and **ab**
27 ,, ,, ,, ,, ,, **Ab** and **aB**

This indicates that the two factors may segregate independently and that segregation can take place either at the first or the second division of meiosis.

Ustilaginales. Dickinson (1931) isolated the four spores of known position in the promycelium of *Ustilago lævis.* The behaviour of the two factors **A** and **B** for sexual fusion as well as the two alternative character pairs (cream *vs.* brown and corrugated *vs.* depressed) were investigated. Utilising the same methods as illustrated above, each character was found to segregate either at the first or at the second division of meiosis.

The work on the Fungi together with the results obtained in mosses supports the view that segregation of the hereditary factors takes place during the meiotic divisions of the nucleus which inaugurate the gametophytic generation. It has also been shown that the factors may segregate from one another at either of the two divisions and not necessarily at that division which reduces the chromosome number from the diploid to the haploid state. Wilcox showed that in *Neurospora sitophila* the incompatibility factors segregated regularly at the second division, but in most other cases it has been found that factors may segregate at either division. Reference should be made to p. 102 for an explanation of this phenomenon in the light of recent work on higher plants.

Xenia. Xenia, or the direct observable effect of the genetic constitution of the pollen upon the young zygote, is reported in *Pisum sativum* (round-wrinkled, yellow-green), Mendel (1865) *Lupinus, Vicia, Linum* and *Phaseolus vulgaris* × *P. multiflorus* (colour of cotyledons) Tschermak (1930). The peculiar process by which endosperm is formed may allow the male parent to express its effect on the characteristics of the fruit. Guignard (1901*a,b*) and Nawaschin (1899) showed that the two nuclei of the embryo-sac fused together to form the central fusion nucleus, prior to fusion with the nucleus of the pollen grain. Weatherwax (1919) reinvestigated the process and showed that sometimes the nuclei did not fuse until the arrival of the pollen nucleus. Two nuclei are furnished by the pollen tube. One fuses with the ovum to form the new zygote, while the other fuses with the central fusion nucleus to form the endosperm. Where the endosperm is not absorbed into the embryo before germination (as in the so-called albuminous seeds), the characters of the endosperm may be analysed. In each cell of the endosperm there is one complement of chromosomes contributed by the male parent and two complements of chromosomes contributed by the female parent.

In accordance with this we find a definite type of factor interaction. For example, there are two races of maize, one with floury endosperm and one with flinty endosperm. When East and Hayes (1911) crossed these two races reciprocally they found that the endosperm of the fruit corresponded with that of the race to which the maternal parent belonged. The hybrid plants produced from the reciprocal crosses, however, were identical, and segregation in the F_2 was similar in both crosses.

If the flinty race carries a factor **F** and the floury race carries the allelomorph **f**, the results may be symbolised thus :—

flinty × floury			floury × flinty		
egg	endosperm	pollen	egg	endosperm	pollen
F	**FF** ×	**f**	**f**	**ff** ×	**F**
embryo	endosperm		embryo	endosperm	
seeds **Ff**	**FFf** (flinty)		**Ff**	**ffF** (floury).	

It will be seen therefore that the embryos from both crosses are of the same constitution but that the endosperms of the reciprocal crosses are of the constitutions **FFf** and **ffF** respectively. The dominance of **F** over **f** is insufficient to cause flintiness in the presence of two doses of **f**. Similarly, the aleurone colour factor **R** is not sufficiently dominant over **r**. Endosperms of the constitution **rrR** (from the cross **rr** × **RR**) are mottled, while endosperms of the constitution **RRr** (from the reciprocal cross **RR** × **rr**) are fully coloured. Xenia has also been reported in rye (von Rumker, 1913) and wheat-rye hybrids (Kattermann, 1932). It is not, however, a general characteristic of endosperm.

Usually, in endosperm, the dominant character is not suppressed by two doses of the recessive factor. For example, endosperm of the constitution **Sususu** or **SuSusu** is starchy, Nixon (1928) found that pollen from different varieties of the date-palm had different effects on the size of the fruit produced by one plant. Swingle (1928) suggested that the embryo and endosperm secreted a substance which influenced the development of the ovary (mother plant tissue). He proposed the term metaxenia for this effect of pollen upon the maternal tissue. Schaffner (1928) points out, however, that xenia is a definite effect of genetic factor balance, and that this supposed metaxenia is physiological in origin. He therefore prefers the term ectogeny in place of metaxenia. Nebel (1930), Nebel and Trump (1932), and Harrison (1931) have reported a similar phenomenon in apples and cotton respectively. Further investigation on this question seems desirable.

LETHAL FACTORS

Geneticists study mainly the behaviour of factors which are recognised by the presence of contrasting allelomorphic factors. They are able to study, for example, the inheritance of flower shape in *Primula sinensis*, but at present they are unable to study the factors causing the presence or absence of the flower itself.

Some factors such as crimp leaf (f) combined with the *sinensis* factor (Ch) have an abnormal effect on various plant characters of *Primula sinensis*. Others reduce the vigour of the plant considerably, *e.g.*, " feeble minded."

Throughout the life cycle a plant is dependent on the genetic material inherited from its parents. Where different allelomorphic factors are present within a species it is reasonable that there should be various degrees of vitality or viability of the genotypes. Hence the so-called lethal factors, which in general are recessive to the normal, can exert their influence at various stages in the life cycle.

Few lethal factors are known which affect gametic viability. Sub-lethal factors are known however, such as those isolated in *Nicotiana Tabacum deformis*, and, to a certain degree, the incompatibility factors. Gametic sterility, which is frequent among plants, is generally brought about by some chromosomal abnormality. Lethal factors affecting the gametes have been suggested in connection with the inheritance of doubleness in Stocks, but it is probable that the lethality is bound up with chromosome structure.

In Stocks, *Matthiola incana*, doubleness is recessive to the single-flowered form. Double flowers are completely sterile. Single-flowered plants may be homozygous for singleness SS,or heterozygous Ss, giving 3 singles : 1 double on selfing. Plants in another strain called " ever-sporting singles " or " d.races " are heterozygous, but on selfing give about 46–47 per cent. singles and 53–54 per cent. doubles. All singles of this strain behave in this manner. Saunders (1911, 1916, 1928*a*,*b*) has also shown that only doubleness is transmitted by pollen of this race. Comparative tests on pollen germination of the above two races of singles have been made by Snow (1924, 1925) and Waddington (1929). Their results indicate that a factor is present in the ever-sporting single race which is lethal to pollen carrying it.

Linked with the factor **S** is a factor **W** for colourless plastids—the recessive **w** gives cream plastids.

A hypothesis has been put forward by Saunders which, although somewhat unorthodox, explains her results remarkably well. Hypotheses involving lethal factors have been advanced by Goldschmidt (1913), Frost (1915), Muller (1918) and Waddington (1929). Waddington adopts two gametic lethals l_w, a pollen lethal and l_s, a pollen and also an egg lethal only active when L_w is present (new terminology for these factors—after Frost, 1931). A pure breeding single white is thus represented $\frac{L_sSL_wW}{L_sSL_ww}$, and an ever-sporting single sulphur white as $\frac{l_sSl_wW.}{L_ssL_ww}$

Crossing over is only supposed to occur between s and l_w. Philp and Huskins (1931) report that in the ever-sporting race, one of the chromosomes carrying the factors for singleness-doubleness (the *A* chromosome) lacks a trabant, l. A pure breeding single white is therefore represented by $\frac{LSW}{LSW}$ and an ever-sporting sulphur white by $\frac{lSW}{Lsw}$. It is considered that l is lethal to pollen containing it, and that on the male side, either l inhibits crossing over between the *A* chromosomes, or the cross-over gametes do not

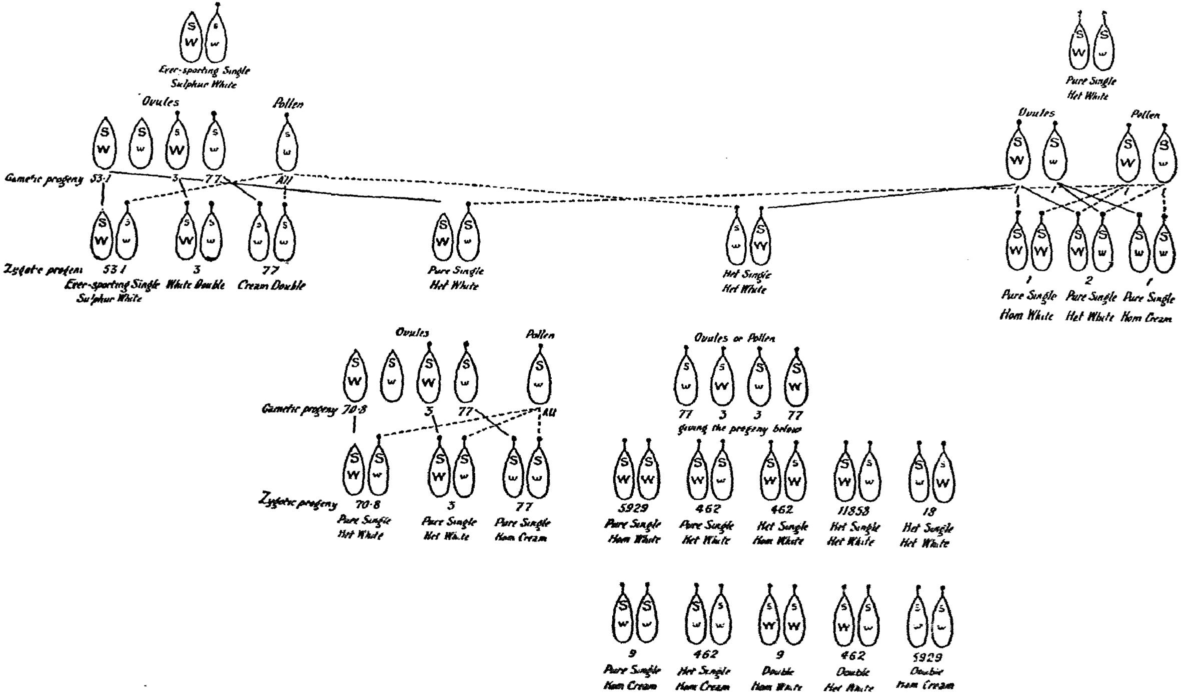

FIG. 14. Diagrammatic explanation of the genetic behaviour of ever-sporting single, pure single and hybrid races of Stock.

function. On the female side crossing over is supposed to take place between the region S and **W** and not between S and l. l is incompletely lethal to eggs and a " Renner Effect " (see p. 269) is suggested. Westergaard (1936) and Kuhn (1938) deny that the ever-sporting race lacks a trabant, and Kuhn is doubtful whether chromosome *A* or chromosome *D* bears the genes considered. Both authors point out that the lethal effect may be seen in the rarity of metaphases and the different quality of fixation in plants carrying the lethal form from those without it.

Fig. 14, while showing the genetic behaviour of the various single-flowered races of Stocks on this hypothesis, also shows their general behaviour.

Saunders' results and the expected proportions on Saunders', Waddington's and the above hypotheses are given in a table by Philp and Huskins (1931). Kvasnikov (1929) and Winge (1931) have found that occasionally the ever-sporting character is lost. This indicates that sometimes crossing over between s and the trabant **L** occurs, or, on Waddington's hypothesis, either double crossing over (see p. 92) between $\mathbf{L}_s$ and $\mathbf{L}_W$ occurs, or crossing over between l_s and S and S and l_w takes place in successive generations.

The young zygote of a plant has to survive under a number of environmental conditions not met with in the rest of the life cycle. The formation of endosperm, the assimilation of the storage products and germination are critical functions which have to be undertaken by the young zygote. The fact that geneticists find genotypes which fail in these respects and are able to study their inheritance is an answer to the objection of some biologists that the science of genetics only embodies a study of less vital characters such as colour, size and shape. Strangely enough some other biologists consider that genetics only involves the study of lethal characters.

Mangelsdorf (1926) and Jones (1920) found seeds of maize with defective endosperm, a character which behaved as a simple recessive to the normally developed endosperm, while Lindstrom (1923) described abortive " flint defective " and " sweet defective " seeds. Demerec (1923) reported " germless " and Eyster (1922) added " scarred," while Wentz (1924) and Garber and Wade (1924) found other types of aberrant development of the seed.

TABLE 8

The Percentage of Germination in Defective Seeds of Fourteen Stocks Compared to the Theoretical Germination of Normal Seeds of the Same Relative Development (*Mangelsdorf* 1926).

Stock.	Defectives.	Theoretical Normal.
de_1	45·6	91·0
de_2	44·9	94·0
de_3	54·0	66·5
de_4	3·5	75·5
de_5	11·2	47·5
de_6	11·8	72·5
de_7	19·6	49·0
de_8	0	49·0
de_9	0	17·0
de_{10}	0	39·0
de_{11}	0·8	22·0
de_{12}	0	10·0
de_{13}	0	12·5
de_{14}	0	3·5

All are genetically controlled by factors which are recessive to normal.

The seeds having defective endosperm exhibit a range in the degree of abnormality. Mangelsdorf isolated fourteen different factors all recessive to normal which gave seeds with a greater or less development of endosperm. The endosperm of these seeds differs from normal endosperm more in quantity than in quality. In no case does defective endosperm attain the size of normal endosperm.

The fourteen factors controlling the character may be arranged in order in proportion to their effect. de_1 gives an endosperm which is half the size of normal and there is a range to de_{12} and de_{14} where only a small fraction of endosperm is found. In all cases the endosperm begins development as in a normal seed, but differences soon appear in the rate of growth of normal and defective seeds. When the factor de_4 is present the embryo is formed, but it disappears apparently by absorption at the same time as the endosperm. The relative stage of development of the endosperm of these fourteen types of seeds at maturity is shown in Table 8.

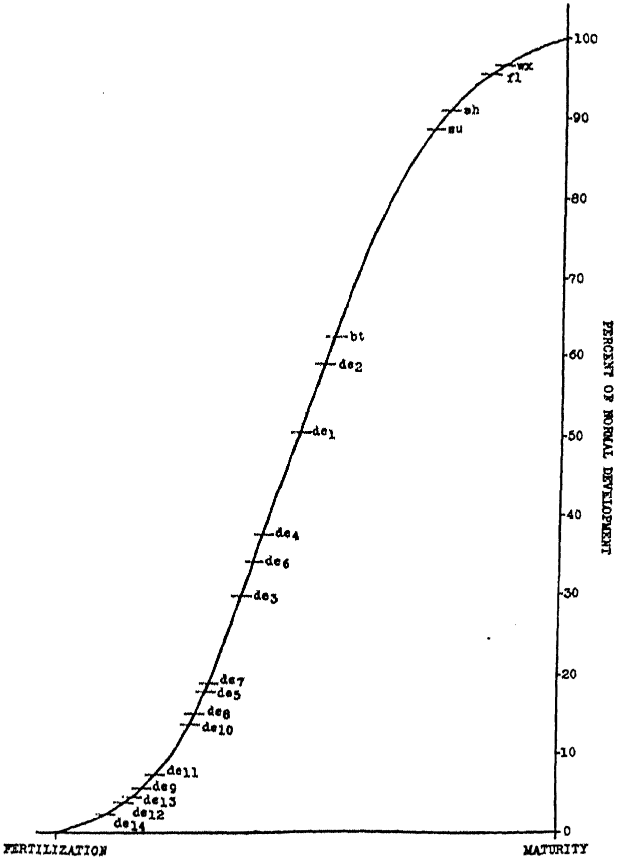

FIG. 15. Diagram in which the relative development of endosperm characters is represented by points on the growth curve of normal seeds of maize.

Any one of these fourteen factors causes one-quarter of the seeds on the ear of a heterozygous plant to be defective. There is also another factor **de$_{pl}$** which causes all the seeds in one quarter of the progeny to have defective endosperm. Thus **de$_1$**—**de$_{14}$** affect the tissues of the zygote early in life, while $\mathbf{de_{pl}}$, is a so-called "plant" factor which affects the sporophyte in such a way that all the seeds produced are abnormal. Mangelsdorf also reports a factor "brittle" which, in expression of texture of endosperm, is intermediate between sugary and "shrunken," and points out that the five characters —waxy, floury, shrunken, sugary and brittle—and the fourteen defective endosperm types can be arranged in order of percentage of endosperm development. The accompanying graph (Fig. 15), is taken from Mangelsdorf (1926). To attain normal seed development, maize must therefore have at least eighteen dominant factors, any one of which in the homozygous recessive condition would reduced endosperm development to a greater or less extent.

This interesting case has another significant feature. The development of endosperm under the influence of factors which do not differ greatly from normal, passes through the stages finally reached by endosperms under the influence of factors lower in the scale. The S shape of the graph is similar to a growth curve and this correspondence may be significant. The expression of some of the factors is qualitatively different (*e.g.*, "waxy," "sugary"), as well as quantitatively different. Linkage studies (see Table of Linkages) show that the various factors are carried on different chromosomes and are not allelomorphic. We cannot say however whether the factors themselves have any phylogenetic connection.

Mangelsdorf (1923, 1926), Lindstrom (1923) and Eyster (1924*b*,*c*) describe recessive factors in maize called "primitive sporophyte" by Eyster and "premature germination" by Mangelsdorf. These factors of which nine or perhaps ten are known, $\mathbf{ge_1}$—$\mathbf{ge_{10}}$ (Mangelsdorf), $\mathbf{pm_1}$—$\mathbf{pm_2}$ (of Eyster), cause the seed to germinate without undergoing a resting period. $\mathbf{ge_1}$, $\mathbf{ge_2}$, $\mathbf{ge_3}$, $\mathbf{ge_4}$ and $\mathbf{ge_5}$ are five independent recessive factors each of which causes premature germination, $\mathbf{ge_6}$ and $\mathbf{ge_7}$ are independent duplicate factors, both being necessary in the recessive condition to give premature germination, while $\mathbf{ge_8}$ and $\mathbf{ge_9}$ are linked duplicate factors. By sectioning the seeds it was found that in seeds containing the premature germination factors, the production of enzymes by the scutellum (to break down the storage materials of the endosperm) began at a very early stage. The resting stage is thus cut out. Although the stocks were known to contain the factors for green seedlings and yellow endosperm, the presence of ge_1, ge_3 or ge_5 in the homozygous recessive condition gave white seedlings and white endosperm. The race with ge_1, which germinated slightly later than the other two, sometimes had a green tinge in the cotyledon. The other factors which had a less intensive effect on the induction of germination gave green seedlings and yellow endosperm. If the factor for premature germination causes enzymes for the breakdown of storage material in the endosperm to act too soon, it will interfere with the action of other factors controlling endosperm or embryo characters.

Oppenheimer (1922) has found that seeds of tomato, gourd, cucumber and *Nicotiana rustica* can be prevented from germinating by surrounding them with crushed tissue of the ovaries of the mother plant or by placing them on filter paper saturated with extract of this tissue. The degree of suppression is approximately proportional to the amount of tissue present or to the concentration of the extract. This effect can be overcome by heating the extract to 100° C. It is suggested that volatile substances may be produced by the mother plant which inhibit germination.

Mangelsdorf found that immature normal seed of maize attached to an ear, when enclosed in a damp cloth, absorbed water but did not germinate. Moistened seeds, from the same ear, placed in an ordinary germinator, germinated in a fortnight, which is a much longer time than dried immature seeds would take. The factors for premature germination may determine the non-production of such an inhibiting substance. From the foregoing it follows that at least twenty-seven dominant factors must be present for the normal development of maize seeds.

The onset of sexual maturity may bring to light some factor which has a lethal effect. A factor such as " bootlace " in tomato causes a deformity of the leaves and of the habit of the plant and assumes importance at gametogenesis by giving abnormal flowers. Honing (1923) describes an interesting case of sub-lethality in *Nicotiana* which illustrates how the growth reaction of a plant of a given genetic constitution varies with the environment.

He found an aberrant form of Deli tobacco in Sumatra cultures which is known as *deformis*. In Sumatra it was characterised by short internodes, deformed leaves and no flowers. It behaved as an incomplete recessive to the normal form and frequently died. Honing brought the stock to Holland and found that this *deformis* grew to twice the size of Sumatra *deformis* and produced fertile flowers. The characteristics were not so extreme in Holland as they were in Sumatra. Honing suggests that there is a single factor difference between *deformis* and normal Deli tobacco and that this factor controls enzyme action, as had been suggested by Goldschmidt (1916), Beyerinck (1917), etc. The reaction of *deformis* and normal tobacco to the different environments certainly supports this view. In the warm conditions of an early season in Holland, Deli flowers before *deformis*, but in a cold season *deformis* flowers first. In the F_1 hybrid between the two types the characteristic leaf deformation does not occur before the eleventh or twelfth node, whereas in the recessive form it is found as soon as the third or fourth node. In both cases the deformation increases in intensity with the ascent of the stem. Honing suggests that the *deformis* plants exhibit greater deformity on account of the earlier start and the greater rate of the enzyme action during development, as compared with the other types.

Whether or not one accepts the hypothesis of the enzyme nature of factor action, it seems probable that the effect of this factor is only sub-lethal because it is interfering with the processes of development occurring normally under Sumatra conditions and possibly such a factor would not be lethal in sub-arctic conditions. *Nicotiana* would not survive under sub-arctic conditions, however, since other factors are present which, under tropical conditions, are either active or passive in the normal mechanism of development.

BALANCED LETHAL FACTORS

If two lethal factors are in one linkage group the condition of balanced lethal factors may be present. Phipps (1929), for example, showed that virescent-8, a lethal virescent recessive of maize, was strongly linked with the factor for tunicate ear which produced sterility when in the homozygous dominant condition. If a plant of the constitution $\frac{v_8tu}{V_8Tu}$ is selfed, it will produce three types of viable zygotes—homozygous dominants, heterozygotes, and homozygous recessives. The recessives will die in the seedling stage on account of the lethality of $\mathbf{v}_8$, while the dominants will be sterile through the sterility of tunicate.

This race of maize, therefore, perpetuates itself only by the heterozygote which is a "balanced heterozygote." A cross-over between $\mathbf{v}_8\mathbf{tu}$ and $\mathbf{V}_8\mathbf{Tu}$ which occurs once in 451 individuals, will give rise to gametes $\mathbf{v}_8\mathbf{Tu}$ and $\mathbf{V}_8\mathbf{tu}$, and the latter type on fusing with a similar type will give a normal homozygote.

Baur (1924) had shown that the aurea variety of *Antirrhinum majus* only existed in the heterozygous condition and on selfing gave 2 aurea : 1 green : 1 non-viable homozygote. He also described a recessive lethal white type. When both aurea and alba were segregating in the same progeny, the ratios obtained were shown by Gairdner and Haldane (1929) to agree with the hypothesis that the factors controlling alba and aurea were linked, the cross-over percentage being about 10%. The double heterozygote $\dfrac{\text{alba } +}{+ \text{ aurea}}$.*, in which it will be noticed that the recessives are repulsed, gave 9·5 yellows : 1 green together with inviable plants. The heterozygote therefore breeds nearly true, as one would expect.

In these two examples the characters which cause the lethality can be recognised and the balanced lethal conditions may be traced. The two factors in maize were closely linked but the expression of each appeared at different points in the life cycle. In the *Antirrhinum* case the linkage was not so close and thus the balanced lethal system broke down more frequently and gave normal green plants.

More usually the factors which are acting in a balanced heterozygote affect the embryo in such a way that one is unable to study the mode of zygote elimination. Nevertheless, the genetic data are often sufficient to show that a balanced lethal mechanism is present. The phenomenon has been studied in various organisms such as *Drosophila*, *Plantago* and *Matthiola*, but it has assumed great evolutionary importance in the balanced heterozygotes of *Œnothera*. Here the self-perpetuation of a species such as *O. Lamarckiana*, which is genetically and cytologically a structural hybrid, depends upon such a mechanism of balanced lethals or upon one closely analogous to it.

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* The + sign beside alba represents the normal allelomorph of aurea and similarly the + sign beside aurea represents the normal allelomorph of alba.

The balanced lethal system enables a heterozygote to be self-perpetuating. The closer the lethals are linked the more efficient the system becomes. Beaded wing in *Drosophila* (Muller, 1917, 1918) is a dominant lethal. While attempts were being made to obtain a stock which was pure for the character Beaded wing, a pure breeding stock appeared suddenly, but it was however of the constitution Bd_1+. The reason for this Beaded wing heterozygote breeding true was the appearance of another lethal closely linked to Beaded wing but on the homologous chromosome, *i.e.*, a balanced lethal system had been set up. Muller points out that if a certain heterozygote is selected by nature or artificially, as in the case of Beaded wing, a lethal will appear sooner or later, by mutation in the required position, to form a balanced lethal system. The frequency of the rate of mutation is high enough in *Drosophila* to make the chance appearance of a lethal in the required position reasonably possible.

Quantitative Inheritance and Heterosis. Action and reaction of genes for quantitative hereditary characters constitute the most critical and least understood of the problems of modern genetics. Whether " such genes operate in general with or without dominance in an additive or multiplicative (geometric or logarithmic) fashion, as do the better known qualitative genes, is quite unknown." Useful data and discussion will be found in Rasmusson (1935), Fisher (1933), Powers (1936), Thomson (1931), Lindstrom (1936), Sinnott and Dunn (1935), Fabergé (1936).

The question of the inheritance of quantitative characters may be similar to that of inheritance of sterility in *Drosophila* (Dobzhansky, 1935), to that of "Minute" in *Drosophila*, of anthocyanin pigmentation in *Dahlia* (Lawrence and Scott Moncrieff, 1935) and to that of sex in plants (Sansome, 1938). In all these cases it is known that several genes in different *loci* contribute to the one effect with sometimes considerable interaction.

The possibly related question of the causes of heterosis or hybrid vigour resulting from crossing individual inbred lines or distantly related forms has been investigated by Ashby (1933, 1937 *a, b, c*), East

(1936), Jones (1918), Luckwill (1937, and in press), Sveshnikova (1936), and others. Ashby has shown that hybrid vigour first shows its effects as an increased size of the embryo in maize and tomato, and that there is no difference in the efficiency index (rate of growth) between F_1 hybrids and the parents. Luckwill has shown that the number of seeds in the fruit and the number of fruits on the truss of a tomato parent are strongly negatively correlated with the size of seed. The physiological results are useful, though complicated, but do not touch the problem of the genetical origin of hybrid vigour. Genes for size differences are known in *Maize* and *Drosophila*. For example, the gene na destroys auxin in maize and the plant is dwarf, and "lazy" plants have an abnormal distribution of hormone; Overbeek (1935, 1938). In *Drosophila* "Tubby" results from the presence of an extra piece of chromosome constituting a fifth linkage group in these flies. Genes for morphological characters are linked with genes for amount of growth in animals (Castle), and in plants (Rasmusson, 1935).

CYTOPLASMIC INFLUENCE ON THE EFFECT OF NUCLEAR FACTORS

Several reciprocal hybrids between species of *Œnothera, Funaria* and *Epilobium* are different in appearance. Some of these differences are known to be due to differential gametic or zygotic viability. Others depend on the interaction of one factor with either of the two different cytoplasms of the parents. The "factors" in the cytoplasm are known as plasmons (Correns, 1909*b*, and Wettstein, 1924*a*).

Several examples of cytoplasmic influence have been found by Wettstein (1924*a*, 1927, 1928) in the mosses. The diploid hybrid sporogonia of *Funaria hygrometrica* × *F. mediterranea* and tetraploid hybrid sporogonia of *F. hygrometrica* × *Entosthodon fasciculare, F. hygrometrica* × *Physcomitrium piriforme, Physcomitella patens* × *Physcomitrium eurystomum* correspond to the female parent in reciprocal crosses. The paraphysis in diploid gametophytes derived from the reciprocal crosses between *F. hygrometrica* × *F. mediterranea* also show the influence of the maternal cytoplasm distinctly. The spores of *F. hygrometrica* × *F. mediterranea* show two size classes in a tetrad of spores (see Fig. 9) but in the reciprocal cross they are of one size class corresponding to that of the maternal parent.

In *Œnothera* there are two main types of reciprocal differences in species hybrids. One is due to heterozygosity and differential viability of the zygotes and gametes (see p. 268). The other is due to differences in the plasmon, and this only will be considered here. If the two normal green species, *O. Lamarckiana* and *O. Hookeri* are crossed, and if the mother is *O. Lamarckiana*, the hybrid *velutina* (see p. 266) is pale green and often dies. Those plants which survive are generally variegated. The reciprocal hybrid *velutina* (*O. Hookeri* × *O. Lamarckiana*) is almost always normal green but a few

TABLE 9.

Cytoplasmic Influence upon Factor Expression in Linum usitatissimum

Plants with cytoplasm from tall ○	☿	M.S.	Plants with cytoplasm from procumbent □	☿	M.S.
F_1 (mm) × MM	175	0	F_1 $\boxed{\text{MM}}$ × mm	188	0
F_2 (Mm) × Mm	126	●	F_2 $\boxed{\text{Mm}}$ × Mm	1,213	341
			expected	*1,165*	*388*
			F_1 $\boxed{\text{Mm}}$ × mm	61	77
			expected	*69*	*69*
			($\boxed{\text{mm}}$ (M.S.) × MM) × mm	62	41
			expected	*51·5*	*51·5*
			$\boxed{\text{mm}}$ (M.S.) × Mm	134	145
			expected	*139·5*	*139·5*
			$\boxed{\text{Mm}}$ × Mm	1,285	422
			expected	*1,272*	*424*

individuals have light green flecks on the cotyledons. *O. suavelolens* × *O. muricata* gives *flavicurva*, which has no chlorophyll, while the reciprocal hybrid (*flavicurva*) is usually green with white spots.

Bateson and Gairdner (1921) found that the cross, procumbent × tall *Linum usitatissimum* gave 25% male steriles in the F_2, while the reciprocal cross gave only hermaphrodites. A male sterile F_2 × tall hermaphrodite gave all male steriles. A male sterile F_2 × procumbent hermaphrodite gave all hermaphrodites and segregation of 3 hermaphrodites to 1 male sterile in the following generation. Male sterile × (T × P) F_1, gave 50% of male steriles and hermaphrodites.

Chittenden and Pellew (1927), Wettstein (1928*a*), Gairdner (1929), Correns (1928*a*) all suggest that the interaction of cytoplasmic and nuclear reactions will account for such differences in reciprocal crosses.

In *Linum* a recessive factor **m** for male sterility may be present in the tall plants which in tall cytoplasm ⊙ gives only hermaphrodites. When the cross procumbent × tall is made the factor **m** may be combined with procumbent cytoplasm □ so that is male sterile and (mm) is hermaphrodite. Table 9, Gairdner (1929), illustrates the expected and observed results in the various crosses.

A similar behaviour is found in *Geranium Endressi* × *G. striatum* and a similar explanation was suggested by Newton (Sansome, 1936). *Satureia hortensis* is a gynomonoecious species. Correns (1928*b*), obtained only hermaphrodites from selfing hermaphrodites and gynomonoecious and hermaphrodites from crossing a female with a hermaphrodite. He suggests that there is a cytoplasmic difference between the two sex forms. Rhoades (1933) also shows that male sterility can be caused by cytoplasmic influence in maize where tests with genes on all the chromosomes showed no linkage with male sterility, and replacement of one chromosome by others did not affect the expression. The maternal line transmitted male-sterility in the presence of any known genes.

East (1932) found that in crosses between *Nicotiana Langsdorffii* and *N. Sanderæ* the self-sterility factors S_{1-15} other than S_I gave rise to male sterile plants when *N. Langsdorffii* cytoplasm was present, and hermaphrodites in the presence of the cytoplasm of *N. Sanderæ*. The factor **Z**, together with the factor $\mathbf{S}_1$, induces the formation of chlorophyll in the corolla of plants with cytoplasm of *N. Langsdorffii*, but not with cytoplasm of *N. Sanderæ*. The combination of factors, **C,P**, **C,D** and **C,D,P**, gives dark anthers in cytoplasm of *N. Langsdorffii* and light-coloured anthers in cytoplasm of *N. Sanderæ*.

In *Epilobium* Lehmann and his students and Akermann (1921) have found many differences in reciprocal hybrids between species. These differences are due to a cytoplasmic effect on the action of genes. The reciprocal crosses between *E. hirsutum* and *E. parviflorum* showed wide differences respecting size of plant, shape of leaves, size of bud, shape of petal, ovaries, fruit and fertility. Michaelis backcrossed *E. luteum* × *E. hirsutum* more than eight times to *hirsutum*, thus obtaining pure *hirsutum* genes in *luteum* cytoplasm. These plants appeared identical with *hirsutem* but did not give differences between reciprocal crosses with *E. luteum*, whereas the original parent *E. hirsutum* produced a large number.

Differences in the characteristics of the protoplasm, such as viscosity, osmotic pressure and effect on chromosome conjugation, have been found in *Lycopersicum*, Schlosser (1935), in *Epilobium*, Hinderer (1936), Groze and Schlenker (1936), in Mosses, Becker (1932).

Sirks (1938) reviews the work on plasmatic inheritance and describes peculiar phenomena in *Vicia Faba*. In addition to factors $\mathbf{C}_1\mathbf{C}_2\mathbf{C}_3$ which cause a difference in the colour of the plants there is a variegation based on one factor **V** which is dominant to **v** for green. Sirks found that segregation into a ratio of 1VV : 2Vv : 1vv was the normal behaviour of typical **Vv** plants, but in cytoplasm of plants with the $\mathbf{C}_3$ (subtypica) factor it was found that **V** was cast out or was not viable in one of the sexes, thus producing a permanent 1**Vv** : 1**vv** segregation. In cytoplasm of variegated plants the **v** factors are eliminated in one of the sexes and an apparently pure breeding strain consisting of **VV** and non-segregating **Vv** plants is produced.

Vicia Faba has been divided into the varieties *major* and *minor*. Sirks found that in the cytoplasm of *major* the segregation of six factors belonging to one linkage group (carried by one pair of chromosomes) was normal. These six dominant factors were introduced from the *major* variety into the cytoplasm of *minor*. No plants homozygous for these six dominant factors were found in the progeny of this hybrid with *minor* cytoplasm. This behaviour was accompanied by about 25% abortion of seeds. Sirks rejects the idea that there is a lethal factor in the chromosome carrying these six factors which acts in *minor* cytoplasm, on the ground that crossing over between the lethal and some of the six factors should have been observed. He puts forward a suggestion that the chromosome bearing this linkage group is impregnated with some lethal character which acts in *minor* cytoplasm. These valuable data of Sirks may possibly be found to be similar to the cases of genotypic control of the chromosomes mentioned by Darlington (1932*b*).

CONCLUSIONS

Consideration of the foregoing facts indicates at once that the original idea of one character—one factor, is false. It will also be apparent that the factors which are isolated by crossing two plants with alternative characters, such as white flowers and red flowers, are only known by their differential effect on that character. Further, their action depends on the presence of many, if not all, of the remaining factors present in the plant.

Naturally, many factors are unknown, since there is either no allelomorph or the different effects of the two have not been detected. The factors which do not show differential action between allelomorphs may possibly be those which are essential for the life and existence of the plant. Indeed, it is probable that many of the lethal factors isolated by genetical study are allelomorphs of these "vital" factors. Sometimes the so-called lethal factor may in reality be an absence of the genetic material. In some cases (sub-lethal factors) the effect in terms of development of the plant can be analysed, but in the more extreme cases the action of the factor is so rapid that the influence of either the lethal factor or the vital allelomorph cannot be analysed.

The development of the plant is dependent on the factors contained in it. At every stage from the original one-celled zygote to the production and survival of the gametes, the development of the plant is controlled by the genetic factors which are contained in the nucleus. Haldane (1932) has given an interesting classification of factors which is based on their time of action. While much more requires to be done in the investigation of the time of factor action, it is apparent that the acceleration or deceleration of the action of a factor creates considerable derangement of the ontogeny (*e.g*, Mangelsdorf's factors for premature germination). The train of factor actions is so balanced that the influence of a factor takes effect at a definite point (or points) in the development of a definite part (or parts) of an organism. Thus the factor h in *Primula sinensis* affects the cotyledons, causing them to be yellowish, and the distribution of the colour in the petals (de Winton unpublished). Another factor which controls length of style acts definitely during the development of the flower. The reactions between the genetical constitution of the plant and the external environment determine the phenotype (or outward appearance and physiological characteristics) of the plant.

CHAPTER II

LINKAGE

Introduction — Crossing-over — Conditions and Theories of Chiasma Formation — Chiasmata and Cross-overs — Coincidence — Conditions of Crossing-over—Genetical and Cytological loci.

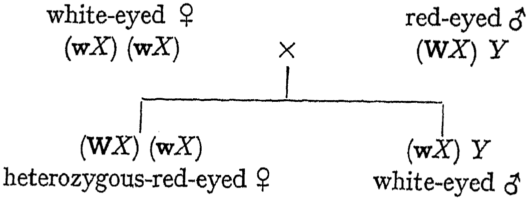
Introduction. The first law of Mendel concerning the separation of factors of one allelomorphic pair corresponds with the cytological behaviour of homologous chromosomes at the heterotype division, but the second law of Mendel, namely, that each allelomorphic pair segregates independently of every other pair, implies that the plant cannot have more pairs of factors than number of chromosomes in the haploid set if factors are borne by chromosomes.

It was soon found, however, that it was necessary to modify Mendel's second law. Bateson and Punnett (1911) (see Bateson, 1930) found that the cross, blue flower (**Bl**) long pollen (**L**) × red flower (**bl**) round pollen (**l**) in the sweet pea produced an F_2 of 177 **Bl L**, 15 **Bl l**, 15 **bl L**, 49 **bl l**, which was certainly not a 9 : 3 : 3 : 1 ratio. They pointed out that such a zygotic series would have resulted from the selfing of an F_1 which produced gametes in the ratio 7 **Bl L** : 1 **Bl l** : 1 **bl L** : 7 **bl l** in place of the ratio 1 : 1 : 1 : 1 when two pairs of factors were completely independent. This phenomenon was called gametic coupling because the dominants (then considered presences according to the presence and absence theory) tended to remain together. Later it was also found that a gametic ratio 1 **Bl L** : 7 **Bl l** : 7 **bl L** : 1 **bl l** was sometimes produced. This was called gametic repulsion, since the dominants tended to repel one another. Bateson and Punnett (1911 *a*, *b*) and Trow (1911, 1912) adopted the reduplication hypothesis in which it was suggested that after segregation there occurred a proliferation of gametes bearing a particular genetic complex.

Later it was found in *Primula sinensis* and other organisms that more than two factors could be linked together at one time.

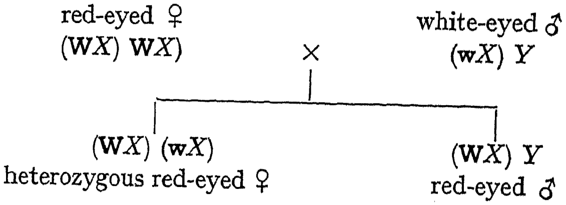
McLung (1902), Wilson and Stevens (see Wilson, " The Cell ") had shown that there was a direct correlation between the morphology of a pair of chromosomes and the sexuality of several animals. The female contained, in addition to other chromosomes, two chromosomes (XX) which were similar to one carried by the male. The male possessed either another dissimilar chromosome or no other extra chromosome. Thus the female was XX and the male either XY or XO in type. Later Morgan (1911) found that sex determination and allelomorphic factors for red and white eyes as well as other factors were associated with this dimorphic chromosome pair in *Drosophila melanogaster*. It was found, for example, that females could be heterozygous for eye colour but males could only be homozygous for white or red eye factors and that linkage between eye colour and sex behaved in a peculiar fashion.

If white-eyed females symbolised by $(\mathbf{w}X)$ $(\mathbf{w}X)$ are crossed with red-eyed males $(\mathbf{W}X)$ Y the F_1 consists of red-eyed females and white-eyed males.



The factors **Ww** are transmitted along with the X chromosome and not independently. The Y chromosome does not contain factors which affect the development of eye colour and therefore the recessive **w** is able to control the colour of the eyes in the male.

The reciprocal cross, red-eyed female $(\mathbf{W}X)$ $(\mathbf{W}X)$ crossed with white-eyed males $(\mathbf{w}X) Y$ gives an F_1 with both males and females red-eyed.



Thus sex determination and several mendelian factors are found to be associated with the behaviour of the dimorphic pair of chromosomes called allosomes, heterochromosomes or sex chromosomes.

Bridges (1913, 1916) found that if, through non-disjunction, an egg obtained two *XX* chromosomes from the female instead of one and fused with an *X* or *Y* from the male, the resulting zygote had two sets of factors of maternal origin instead of the normal one. In Lepidoptera, birds, some fishes, forms of *Silene Otites* and *Fragaria*, the female sex is the heterozygous sex usually symbolised by *WZ* and the male sex is *ZZ*.

Morgan (1911) suggested that the facts of linkage could be brought into line with the chiasmatype theory of Janssens (1909) if the factors were placed in a row on the chromosomes in such a way that the position of the factor of paternal origin on the paternal chromosome corresponded to that of the allelomorph of maternal origin on the chromosomes derived from the mother.

If the factors are situated on the chromosomes they should exhibit segregation phenomena of a specialised form in correspondence with the cytological facts. All factors on one chromosome should segregate independently of those on non-homologous chromosomes. The factors on one chromosome should show complete linkage unless breaks in the chromosome occur between the loci of the factors.

Obviously also, for genetical requirements, a breakage must take place at meiosis at a corresponding time and place on the two homologous chromosomes. This must be followed by interchange of the broken ends to account for the recombination products of the factors. For example, if one chromosome bore the dominants **A** and **B** while the homologue bore the allelomorphs **a** and **b** in similar positions, normal disjunction of these chromosomes without interchange of parts would give gametes with the parental complements **AB** and **ab**. With interchange of the parts of chromosomes at a position between the loci of **A** and **B**, " new " chromosomes would be formed with the factorial constitution **Ab** and **aB**. These new chromosomes contain the factors in the recombined or crossed-over form.

The recombinations **Ab** and **aB** will occur with a frequency proportional to the number of breaks and rejoins. For example, the genetic output, in *Lathyrus odoratus* was 7 **Bl L** : 1 **Bl l** : 1 **bl L** : 7 **bl l**, or 2 character recombinations (**Bl l** and **bl L**) in sixteen plants, *i.e.*, 12·5%. The crossing-over percentage of the genes may also be expressed as the cross-over value 0·125. Sturtevant (1913) realised that if the genes were placed linearly on the chromosome the cross-over values would be related to one another in an additive manner. If the cross-over value between genes **A** and **B** was 3% and between **A** and **C** was 4% the cross-over value between **B** and **C** would either be 1% or 7% depending on whether the order was **ABC** or **ACB**. The relative distances of the genes one from another would thus be a function of cross-over values. He found that this was the case when the cross-over values were small.

Working data on crossing-over may be understood by considering the **C sh wx** example in Table 12. The corresponding pairs of allelomorphs are **C** +, **sh** +, **wx** + · *i.e.*, + represents **c**, **Sh** and **Wx**, respectively. Recombinations in region 1 are the individuals which are **C** + + and + **shwx** in constitution, *i.e.*, they have resulted from gametes crossed over between the loci of **c** and **sh**. Therefore the ratio for **c** and **sh** is ++ 2708 : + sh 113 : C + 116 : C sh 2538. The cross-over value equals — $\frac{113 + 116}{\text{total}} = 0{\cdot}034$. Mather (1938) gives methods for calculating linkage and errors of estimation.

The following list of genes and linkage values in plants includes the more important data. It will be seen that the greatest number of genes and their relationships have been investigated in maize. The table of linkage groups in plants gives under each chromosome the order and distances of well-analysed genes.

TABLE 10

Genes in maize (Emerson, Beadle and Fraser, 1935).

When the character expression of the gene is dominant to the normal stock the gene symbol has a capital letter. The chromosome on which the gene is located is indicated by the number of the chromosome, thus C. 1. If the chromosome is unknown this is indicated by C. u.

a$_1$	anthocyanin colour of plant, aleurone and pericarp, allelomorph series, C. 3.
a$_2$	anthocyanin, complementary to **Aa$_1$** in plant and aleurone colours, C. 5.
a$_3$	anthocyanin, C. 10.
ad$_1$	adherent leaves, bracts and inflorescences, C. 1.
ad$_2$	leaves adhere in young stage, C. not known.
al	albescent, seedlings turn white, C. not known.
an$_1$	anther ear—1, anthers in pistillate inflorescence, C. 1.

Maize—continued.

an_2	anther ear—2, C. not known.
ar	argentea, yellow striations in leaf, C. 9.
as	asynaptic, lack of pairing at meiosis, C. 1.
at	antherless, C. not known.
au_1	yellow seedling, lethal, C. 9.
B	Booster, intensifies colour, allelomorphic series, C. 2.
ba_1	barren stalk, no pistillate inflorescence, C. 3.
ba_2	barren stalk, C. 2.
bd	branched silkless, C. 7.
Bh	blotched aleurone in presence of AcR, C. 6.
bk	brittle stalk, leaves and stems brittle, C. not known.
bl_1	blotched leaf, necrotic areas in leaf, C. not known.
bl_2	,, ,, ,, ,, ,, ,,
bm_1	brown midrib, C. 5.
bm_2	,, ,, C. 1.
bm_3	,, ,, C. not known.
Bn_1	brown aleurone, pale yellow aleurone, C. 7.
bn_2	,, ,, ,, ,, ,, C. not known.
bp	brown pericarp in presence of P, C. 9.
br	brachytic, nodes shortened, C. 1.
bs	barren sterile ; very few flowers, C. not known.
bt_1	brittle endosperm, C. 5.
bt_2	,, ,, C. not known.
bt_3	,, ,, C. not known.
bv	brevis, plant about half normal height, C. 5.
C	aleurone colour, C. 9.
cb	chloroblotch, C. 5.
Ch	chocolate pericarp, C. 5.
cr_2	leaves crinkled, C. 3.
d_1–d_7	non-allelomorphic, dwarf plant, C. 3, 3, 9, u, 2, 5, 10.
de_1–de_{16}, def	non-allelomorphic, defective endosperm, C. 4,u, u, u, u, 4,u, u, u, u, u, u, u, 9, 4, u, u, 10.
dl	dull brown endosperm, C. not known.
dm	dead margin at base of upper leaves, C. not known.
Dt	dotted aleurone, C. not known.
du	dull endosperm, C. 10.
f_1–f_3	non-allelomorphic, fine white stripe on leaves, C. 1, 5, 10.
fi	fine streaks on leaves, C. 6.
fl_1 fl_2	non-allelomorphic, floury endosperm, C. 2, u.
fr_1 fr_2	duplicate genes for fraying of leaf edges, C. 7, 7.
fs	fasciated ear, C. u.
g_1–g_4	non-allelomorphic, golden, C. 10, u, 9, 9.
Ga	gametophyte, reduces vigour of pollen, C. 4.
gc	glucostachous, plant unable to use sugars, C. not known.
ge_1–ge_{15}	non-allelomorphic, premature germination, Cs. unknown.
gl_1–gl_{10}	non-allelomorphic, glossy leaves, C. 7, 2, 4, 9 (?), 5, u, u, 5, u, 1, 9.
gm_e, gm_1–gm_4	germless, C. 9, 9 (?), 10, u, 6.
gs_1, gs_2	non-allelomorphic, green-striped, C. 1, 2.
h	soft starchy endosperm, C. u.
hf	hermaphroditic flowers, C. u.
Hs	hairy leaf-sheath, C. 7.
I	inhibitor of aleurone colour, C. 9.
ij	Iojap striping, C. 7.
in	intensifier of aleurone colour, C. 7.
j_1 j_2	non-allelomorphic, japonica striping, C. 8, 4.
knob	structure at end of C. 9 in some strains.

Maize—continued.

l_1–l_7	non-allelomorphic, lutescent, C. 10, 10, u, 10, 5, 9, 9.
la	lazy plant, mature plants lie down, C. 4.
lg_1–lg_2	liguleless leaf, C. 2, 3.
li	lineate stripes on the leaves, C. 10.
lo	lethal ovule, ovules abort, C. 4.
lp	pollen lethal, C. 5.
Md	midcob colour, pith of cob coloured, C. u.
me	mealy endosperm, C.u.
mi	midget, plant small, C. u.
ms_1–ms_{20}	non-allelomorphic, male sterile, C. 6, 9, 3, u, u, u, u, 8, u, u, u, u, u, u, u, u, 1, 5, 9, 9.
Mt	mottled aleurone, C. 10.
na–na_2	non-allelomorphic, nana dwarf, C. 3, u.
nl_1–nl_2	non-allelomorphic, narrow leaf, C. 10, u.
o_1–o_2	opaque endosperm, C. u, 7.
oy	oil-yellow plant, C. 5.
P	allelomorphic series, pericarp and cob colour, C. 1.
pb_1–pb_4	non-allelomorphic, piebald patches on leaves, Cs., u.
Pc_1–Pc_4	non-allelomorphic, purple colorrhiza, C. 9 (?), 10, u, u.
pg_1–pg_{10}	non-allelomorphic, pale green seedlings, C. 10, 3, 7, u, u, 9, 5, u, u, u.
pi_1–pi_2	non-allelomorphic, secondary pistillate flowers, Cs. u, .
pk	polkadot leaves, C. 9.
Pl	purple plant colour, C. 6.
pm	pale midrib, C. 3.
po	polymitotic, abnormal meiosis, C. 6.
pr_1	red aleurone, C. 5.
Pr_2	purple aleurone, C. 9.
ps	panicle developed at second or third node, C. u.
Pu_1–Pu_2	purple plumule, Cs. u.
py	pigmy, C. 6.
R	coloured aleurone and plant, many allelomorphs, C. 10.
ra_1–ra_2	ramosa ear, branched, C. 7, 3.
re_1–re_4	reduced endosperm, C. 5, 5, 9, 4 (?).
Rg	ragged leaf, C. 3.
ro	rolled leaves, C. u.
Rp	rust resistance, C. 10 or absent.
rt	rootless (secondary roots weak), C. 3.
S_1–S_2	coloured scutellum, non-allelomorphic C. 4, u.
sa_1–sa_2	striped auricles, non-allelomorphic, C. 9, 5.
sc_1–sc_2	scarred endosperm, non-allelomorphic, C. 5, 9.
sf	stiff leaves, C. 5.
sh	shrunken endosperm, C. 9.
si_1–si_3	supernumerary silks, non-allelomorphic, C. 6, u, u.
sk	silkless, female sterile, C. 2.
sl	slashed leaves, C. 7.
sm	salmon silk, C. 6.
sp	small pollen, C. 4.
sr	striated leaves, C. 1.
st	sticky chromosome, meiosis irregular, C. 4.
su_1–su_3	sugary endosperm, non-allelomorphic C. 4, 6, 9.
sy	yellow scutellum, C. u.
tn	tinged plant, C. 5.
Tp	many nodes and tillers, narrow leaves, C. 7.
ts_1–ts_5	non-allelomorphic Ts 3 and Ts 5 dominants, tassel seed, terminal inflorescence affected, C. 2, 1, u, 3, 4.
Tu	tunicate ear, glumes long, C. 4.

Maize—continued.

tw_1–tw_3	twisted seedling leaves, non-allelomorphic Cs. u.
v_1–v_{20}	virescent seedlings, non-allelomorphic C. 9, 5, 5, 2, 7, 6, 6, 4, u, u, u, 5, u, 9, 9, u, u, 10, u, 10.
va_1–va_2	variably sterile, C. 7, u.
vp_1–vp_4	viviparous, C.10, 5, 4, 9.
w_1–w_{12}	white seedling, non-allelomorphic, C. 6, 10, u, 4, 6, 6, u, u, u, u, 9, 4.
wa	warty anthers, C. u.
Wh	white endosperm, C. 7.
wl	white leaf base, C. 4.
ws_1–ws_3	white sheath, non-allelomorphic, C. u, u, 2.
wx	waxy endosperm, C. 9.
xn_1–xn_2	xantha seedling (yellow), C. 10, u.
Y_1–Y_2	yellow endosperm, non-allelomorphic, C. 6, 5.
yd	yellow dwarf, C. 6.
yf	yellow flecked seedling, C. 9.
yg_1–yg_3	yellow green plant, non-allelomorphic, C. 5, 9, u.
Yp	pale yellow endosperm, C. 7.
ys_1–ys_2	yellow striped leaves, C. 5, 2.
yt	yellow top, C. 3.
zb_1–zb_5	zebra striped, transverse striped leaves, non-allelomorphic, Cs. u.
zg_1–zg_3	zig-zag culm, C. u, 1, 6 (?).
zl	zygotic lethal, C. 1.

TABLE II

Some Linkage Groups in Plants

Antirrhinum majus.	I. **Phan**, 29 **Marm**, 7 **Mus**, 5 **Cus**, 2 **Aur**, 3 **Opa**, 12 **Alb**. (Schick, 1933).
	II. **Uni**, 9 (?) **Dich**, 10 (?) **Comp**, 7·5 **Pal**, 11 **Pary**. (Schick, 1933).
	III. **Deci**, 38 **Luv** ? **Phyl**, 30 (?) **Stri**. (Hackbarth, 1933).
Brassica oleracea.	Malinowski (1929).
Collinsia bicolor.	Hiorth (1933).
Glycine Soja.	Owen (1927).
Lathyrus odoratus.	Punnett (1925).
Lupinus angustifolius.	Hallquist (1921).
Lycopersicum esculentum.	I. **d_1**, 5 **p**, 14 **o**, 18 **s**, 10 (?) **W_o**. (MacArthur, 1934).
	V. **f**, 25 **a**, 33 **lf**.
Matthiola incana.	Saunders (1928).
Oryza sativa.	Chao (1928).
Papaver Rhoeas.	Philp (1933).
Pharbitis Nil.	Imai (1931,*a*,*b*.)
Pisum sativum.	Winge (1936).

Primula sinensis. I. **S**, 6·2 **B**, 18·4 **X**, 22·4 **G**, 3·6 **L**.
II. **P**, 15 **WF**, 10 **CH**.
III. **M**, 22·8, **Y**, 7·69 **H**, 5·34 **K**.
IV. **O**, 23·8 **Mp**. (de Winton and Haldane, 1933, 1935).

Tropaeolum. Moffett (1937).
Vicia Faba. Sirks (1933).

Zea Mays. Emerson, Beadle and Frazer (1935).

Chromosome 1. Length 128 units.
P25 **as** 27 **br** 5 **f**$_1$ 17 **an**$_1$ 27 **gs**$_1$ 27 **bm**$_2$.
Associated with **P** : **ts**$_2$, **zl**, **ms**.
an$_1$: **ad.**$_1$
gs$_1$: **zg**$_2$.
Involved in T_1–2a near **an**$_1$–**f**$_1$ (semi-sterile 1).
T_1–6a ,, **br**–**as** (,, 5).
T_1–6b ,, **br** (low sterile).
T_1–7a ,, **br**–**f**$_1$ (semi-sterile 3).
Also involved in translocations with chromosomes 3_4, 4_1, 5_3, 7_4, 9_3, 10_2.

Chromosome 2. Length 73 units.
lg$_1$ 19 **gl**$_2$ 19 **B** 7 **sk** 12 **fl**$_1$ 6 **to**$_1$ 8 **v**$_4$.
Associated with **lg**$_1$: **ws**$_3$.
gl$_2$: **d**$_5$ **gs**$_2$.
ts$_1$: **ba**$_2$.
Involved in T_1–2a beyond **v**$_4$ (semi-sterile 1).
T_2–5a near **ts**$_1$ (semi-sterile 4).
Also involved in translocations with chromosomes 3_3, 4_4, 5_1, 6_5, 7_3, 8_1, 9_2, 10_1.

Chromosome 3. Length 103 units.
a$_1$ 28 **na**$_1$ 11 **ba**$_1$ 17 **ts**$_4$ 7 **Rg** 22 **d**$_1$ 18 **cr**$_1$.
Associated with **ts**$_4$: **pm**$_1$ **pg**$_2$.
ba$_1$: **lg**$_2$.
Rg : **ra**$_2$.
cr$_1$: **ms**$_3$, **yt**.
Involved in translocations with chromosomes 5_3, 6_2, 7_2, 8_2, 9_2, 10_4.

Chromosome 4. Length 111 units.
de$_1$ 35 **Ga** 21 **Ts**$_5$ 10 **sp** 3 **lo** 2 **su**$_1$ 3 **de**$_{16}$ 26 **Tu** 5 **j**$_2$ 6 **gl**$_3$.
Associated with **Ts**$_5$: **la st wl**.
Tu : **v**$_8$.
su$_1$: **S**$_1$ **vp**$_3$.
Involved in translocation with chromosomes 5_4, 6_3, 7_1, 8_1, 9_2, 10_2.

Zea Mays—continued.

Chromosome 5. Length 72 units.

↑ a_2 6 bm_1 6 bv 19 pr_1, 9 ys_1 32 v_2.

Associated with bm_1 : bt_1 vp Y_2 v_3 (?) sf tn.

pr_1 : v_{12} d_6 sc_1.

Involved in T2–5a ↑ —bm_1 (semi-sterile 4).

T 4–5a.

T 5–7c.

Also involved in translocations with chromosomes 6_1, 7_2, 8_1, 9_1, 10_1.

Chromosome 6. Length 61 units.

po 13 Y_1 28 Pl 10 sm 10 py.

Associated with Y_1 : si_1 fi ms_1 yd w_5 w_6.

Unknown positions : Bh su_2 v_6 v_7 gm_4 w.

Involved in T1–6 b near Y_1 (low sterile).

T1–6a (semi-sterile 5).

T6–9a.

Also involved in translocations with chromosomes 8_1, 9_1 10_1

Chromosome 7. Length 52 units.

v_5 14 ra 4 gl_1 10 Tp 6 ij 18 Bn_1.

Associated with ij : fr_1 sl.

gl_1 : fr_2 in.

Bn_1 : pg_3.

Positions unknown bd Hs O_2 Wh Yp.

Involved in T1–7a ra ↑ —gl (semi-sterile 3).

T5–7a beyond Bn_1 (semi-sterile 6).

Also involved in translocations with chromosomes ^{1}.

Chromosome 8. Length 18 units.

j_1 18 ms_8.

Involved in T_8–9a between ↑ —j_1 (semi-sterile 2).

Also involved in translocations with chromosomes 9_1, 10_4.

Chromosome 9. Length 65 units.

Knob 1·5 yg_2 19 C3 sh 15 bp 15 wx 12 v_1.

Associated with C : 1 Da l_6.

wx : au_1 de_{15} v_{15} ar d_3 l_7 w_{11}.

yg_2 : re_3 g_4.

Unknown positions : cr_2 gl_4 gm_e ms_2 sa_1 sc_2 yh.

Involved in T6–9a wx–v_1.

T8–9a v_1 4 (semi-sterile 2).

Chromosome 10.

nl_1 18 gv 14 R.

Unknown positions R. l_2 d_7 w_2 Pc_2 zb_2 du_1 a_3 gm_2.

li . pg_1 l_4 vp_1 def, f_3, v_{18}, v_{20} xn_1 Rp.

Involved in translocation with chromosome 9_1.

Sufficient data are now available in several organisms to construct maps of chromosomes which indicate the relative position of the genes one to another and in some cases to fixed cytologically determined points. Fig. 21 of *Drosophila melanogaster* only include those genes which are easily identified by their character expression and do not include the many lethal and modifying genes which are known. The genetic maps of the chromosomes of *Drosophila melanogaster* cover almost all the active regions of the chromosomes whereas all the chromosomes of maize are known to be larger than the lengths given in the genetical maps. The presence of translocations in maize, *Drosophila* and *Pisum* is providing great aid in mapping the chromosomes (see p. 263).

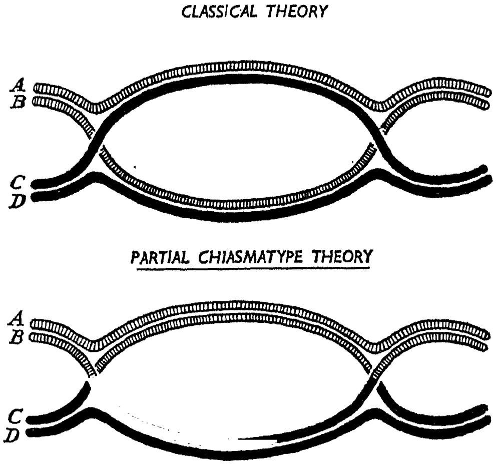
THEORY OF CHIASMA FORMATION

Cytological evidence of many types shows that the breakage and reunion of the chromatids is a normal and essential phenomenon of meiosis (see Darlington (1937) under "interlocking," "unequal bivalents," "inversions," "structural hybrids," "structural change"). The exact mechanism of crossing-over depends on the manner in which chiasmata are formed.

Classical Theory. There are two views regarding the method of formation of a chiasma. The classical theory (*cf.* Robertson (1916), Wenrich (1917), Wilson (1925), Seiler (1926) and Bělăr (1928)) is that the constituent chromatids do not break to form a chiasma. Thus chromatid A in Fig. 16 may pair with B, and C with D, at one point of the length and at another A may pair with C, and B with D. The point of change of the pairing association is a chiasma. At what stage the segmental interchange necessary for genetical crossing-over takes place is a matter for dispute among the holders of the classical theory. The reduction in the number of chiasmata between diplotene and metaphase is attributed to their resolution by breakage while the configurations at metaphase indicate to Prell (1923) and Chodat (1925) that interchange may take place at the time of chromosome disjunction. If reduction in chiasmata by breakage occurred, genetical results of crossing-over in *Pisum sativum* where the number of chiasmata at metaphase is high, should be entirely different from that of *Primula sinensis* where the number of chiasmata is considerably reduced by the time of metaphase. Differences in the crossing-over values of this magnitude have not been observed.

Chiasmatype Theory. An alternative theory of chiasma formation and segmental interchange which appears to be supported by evidence of a diverse nature is that put forward by Janssens (1924). Belling (1928*a*) and Darlington (1930*b*, 1931*a*, 1931*c*).

Janssens (1909) supposes that chiasma formation results from a previous segmental interchange (reciprocal transverse breaking and fusion between the chromatids). He suggests various forms of chiasmatype. In total chiasmatype all four chromatid strands interchange at one corresponding point in their length; in partial chiasmatype only two chromatids interchange at any one point in the chromosome length. He also suggests that chiasmatype might occur at metaphase or at the second division, and that certain configurations in mitotic divisions might be of the same nature. Since genetic evidence indicates that normal crossing-over takes place during prophase of the first division, the partial and total chiasmatype hypotheses are of direct interest to the geneticist (see pp. 84, 97).


CLASSICAL THEORY

PARTIAL CHIASMATYPE THEORY

FIG. 16. Chiasma formation.

Belling (1928*a*) and Darlington (1930*b*) independently put forward views which are essentially the same as the partial chiasmatype theory of Janssens. Darlington suggests that total chiasmatype does not occur, while Belling assumes it to be very rare.

In Darlington's words (1930*b*), " a chiasma is constituted by genetical crossing over between two of the four chromatids taking part in it, and association at diplotene is between chromatids derived from the same chromosome." These two assumptions enable the genetical and cytological data to be brought into line.

Fig. 16 represents a bivalent immediately after chiasma formation at diplotene and illustrates the difference between this view and the classical view.

It will be seen that on the classical view each chromatid has not changed in structure but remains similar to the structure of the original somatic chromosome until segmental interchange takes place later. On Janssens' theory, however, a chiasma is formed, as a result of crossing-over of two of the four chromatids and the resulting chromatids are not similar to those of the somatic complement. It should be said at once that both of these theories are in agreement with various cytological observations, but lead to different requirements in subsidiary hypotheses.

SEGMENTAL INTERCHANGE AND GENETICAL CROSSING-OVER

Proof that chromatid segmental interchange is associated with chiasmata formation and that it is the mechanical means for genetical crossing-over has been afforded in different ways by Darlington (1930*b*, 1932*a*), Stern (1931), McClintock (1931), McClintock and Creighton (1931), Mather (1933), Sansome, E. R. (1932), Rhoades (1935), Brink and Cooper (1935), etc.

In the discussion of these cases it will be seen that there is no definite evidence as to the mode of crossing-over between chromatids. Nevertheless, the theory of partial chiasmatypy affords in every case a simpler and more satisfying explanation than the alternative theory.

Darlington (1931*b*) and Sansome, E. R. (1932) found associations of chromosomes with a configuration of a figure-of-eight in structural hybrids of *Œnothera* and *Pisum*. A structural hybrid can result from crossing two races which differ in the arrangement of the parts or segments of chromosomes. [For example, one race may have the somiatc chromosomes *AB, AB, CD, CD, EF, EF*, etc., while the other race has *AC, BD, AC, BD, EF, EF*, etc. The chromosome segments *A, B, C, D*, are united in the two races to form different chromosomes—relatively interchanged chromosomes. In the hybrid between these races the chromosomes will be *AB, BD, DC, CA, EF, EF*, etc. Since homologous parts pair, a ring of four chromosomes, $\underbrace{{}^{AB}\diagdown_{BD}\diagup^{DC}\diagdown_{CA}}$ will be formed in this diploid species at meiosis.] Rings consisting of larger numbers of chromosomes will be formed when more chromosome segments are interchanged. For example, some *Œnothera* species have all the fourteen chromosomes in one ring.

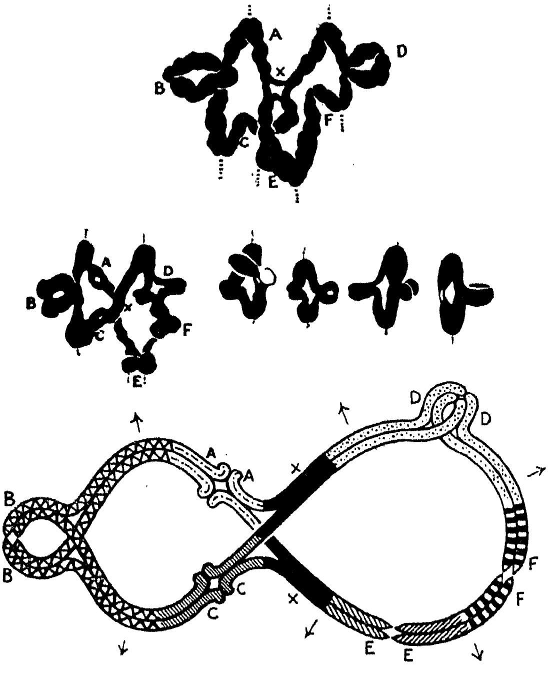


FIG. 17. Figure-of-eight configurations with chromatid segmental interchange and diagram of the genetical interpretation. (Sansome, E. R., 1932.)

The "figure-of-eights" found by Darlington in species of *Œnothera* and by Sansome in a ring of six chromosomes in *Pisum* are proofs of cytological segmental interchange for the following reasons. In the diagram (Fig. 17) representative of both *Pisum* and *Œnothera* (in *Œnothera* there are more chromosomes involved in distant parts of the ring) it will be seen that a chiasma is present between the segments x of chromosomes AxD, CxE, and that in every case homologous parts represented by letters are pairing. This configuration cannot arise by any other method than that segmental interchange has occurred in segment x between chromatids AxD and CxE, giving rise to new chromatids AxE, CxD, if homologous parts only pair, since in the normal diploid there are only two of every part.

On the chiasmatype theory with the formation of chiasmata resulting from breakage and reunion, no further hypothesis is required to account for these facts. On the alternative view it is necessary to assume that chiasmata of the compensating type (see p. 91) have been previously formed, and that chromatid interchange has occurred between them. But since Sansome (1932) finds that the chiasma occurs at the x segment in 78% of cases, this assumption involving special types of chiasmata seems unlikely.

The above case demonstrates crossing-over between chromatids without the use of genetical data. In *Zea* and *Drosophila* the demonstration illustrates genetical and cytological crossing-over taking place in one individual to give one product. The normal female, *Drosophila melanogaster*, has two similar rod-shaped sex chromosomes XX in addition to the autosomes, while the male has one sex chromosome X similar to that of the female together with a v-shaped chromosome Y which has a sub-median attachment constriction dividing it into a longer and a shorter arm. Stern (1931) synthesised female flies of the constitution X^p, X^d, $\overset{\frown}{XY}{}^1$, in which X^p and X^d were separate proximal and distal halves of an X chromosome, and $\overset{\frown}{XY}{}^1$ was composed of an X joined to the long arm of the Y chromosome, the shorter arm being absent. When one half of the broken X chromosome carried the factor **B** (Bar eye) at 57·0 units (see p. 98) and **cr** (carnation) at 65·0 units and the compound chromosome $\overset{\frown}{XY}{}^1$ carried the wild

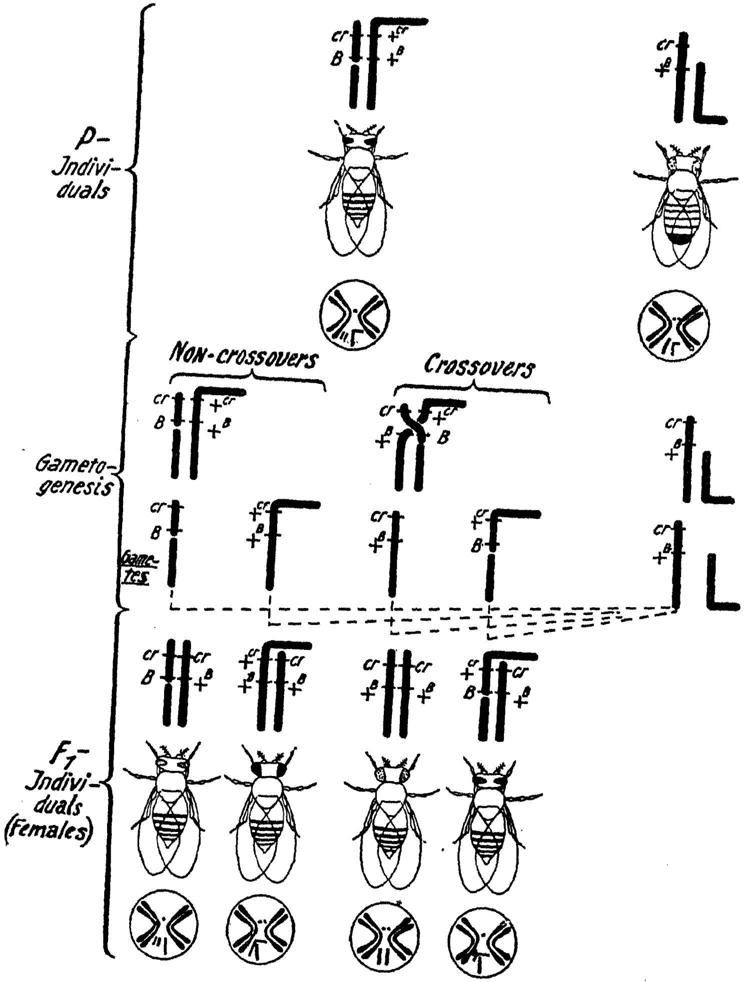


FIG. 18. Diagram of the genetical and cytological constitution of an individual of *Drosophila melanogaster* with a fragmented *X* chromosome and of its progeny. (Stern, 1931.)

type allelomorphs, crossing-over would influence the recombination of the factors and the structure of the chromosomes. Fig. 18 shows the gametic output of such a fly together with the zygotic types obtained on crossing to a normal male carrying cr and wild type factors.

A cytological examination was made on 364 individuals of the progeny. In 156 cases the factors B and cr had crossed over and in every case the chromosome parts were observed to have interchanged. Where no genetical crossing-over took place between the factors (203 individuals) there was no observed segmental interchange (see also p. 252 and McClintock (1931), Rhoades (1935)).

Conditions of Chiasma Formation and Genetical Crossing-over. It was stated earlier that, in general, chiasmata were formed at random along the chromosome length with a frequency proportional to the length. This is certainly not the case in short chromo-

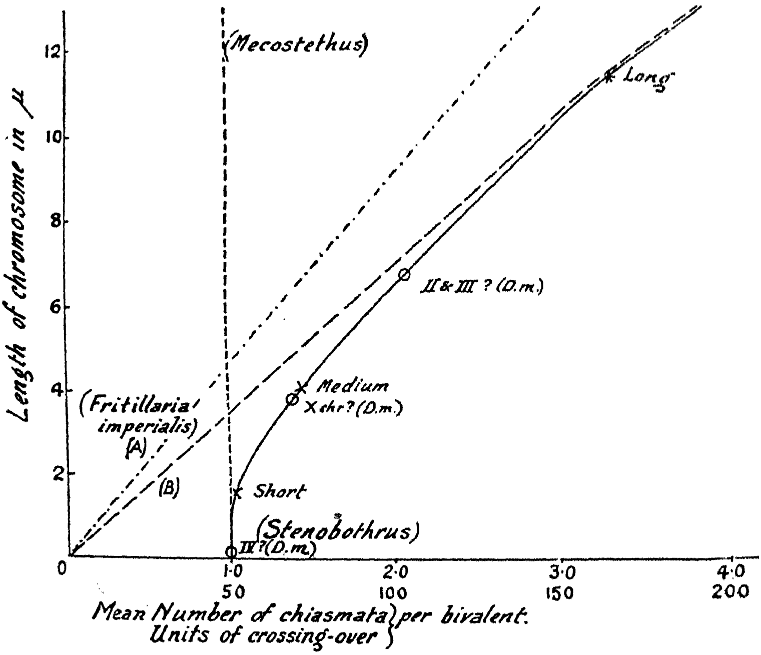


FIG. 19. Graph showing three types of relationship possible between chiasmata or crossing-over and the length of the chromosomes: direct proportion in *Fritillaria imperialis* (two clones); fixed value with localisation in *Mecostethus* and perhaps in some *Tettigidæ*; the compromise in *Stenobothrus* and perhaps in *Drosophila melanogaster* " *D.m.*" (From Darlington and Dark, 1932.)

somes but may be correct for chromosomes above a certain length which are not affected by the presence of large inert regions as in *Lycopersicum* (Lesley and Lesley, 1936), or influences external to the chromosome. Fig. 19, from Darlington and Dark (1932), illustrates the chiasma frequency of different chromosomes in *Stenobothrus lineatus*, together with that of *Fritillaria imperialis* and the genetic lengths of the chromosomes in *Drosophila melanogaster*. In *Stenobothrus* the chiasma frequency is proportional to the length; but a decrease in chromosome length leads towards a frequency of one chiasma in place of no chiasmata. There is a good agreement also when the genetic data from the *X*, *II* and *III* chromosomes of *Drosophila* are superimposed on the figures from *Stenobothrus*. Chromosome *IV* in *Drosophila* has a minimum of 1 chiasma, *i.e.*, the chiasma frequency is high in proportion to its length.

In *Fritillaria meleagris* (Darlington, 1932 *b*) only one chiasma is formed in each arm of a chromosome irrespective of its length. The frequency of chiasmata depends on (1) the pairing properties of the chromosomes at zygotene; (2) the segmental interchanges possible in these parts that have paired. This latter condition is influenced by (*a*) the relative times of the pairing of the chromosomes (see Darlington, 1937, p. 288) and of the onset of chiasma formation; (*b*) interference between chiasmata in one pair of chromosomes; (*c*) a suggested possible interference in chiasma formation between different chromosomes (see Mather, 1936); (*d*) presence of inversions, translocations and other changes of homology near paired chromosome parts; (*e*) gene control; (*f*) influence of the centromere, and ends of the chromosome arm on (1) chromatid splitting, (2) the formation of the proximal chiasma.

Relationship of Chiasma Formation and Crossing-over. Belling (1931), followed by Sax (1932) and Mather (1933), has utilised a formula connecting cross-overs with chiasmata (see Weinstein (1936) for general treatment). A consideration of Fig. 16 will show that at one chiasma there are to two cross-over chromatids and two non-cross-over chromatids, *i.e.*, 50% crossing-over. Fig. 20 shows the possibilities where two chiasmata are formed. Either the chromatids which take part in the first chiasma also take part in the second (reciprocal) or neither take part in the second (comple-

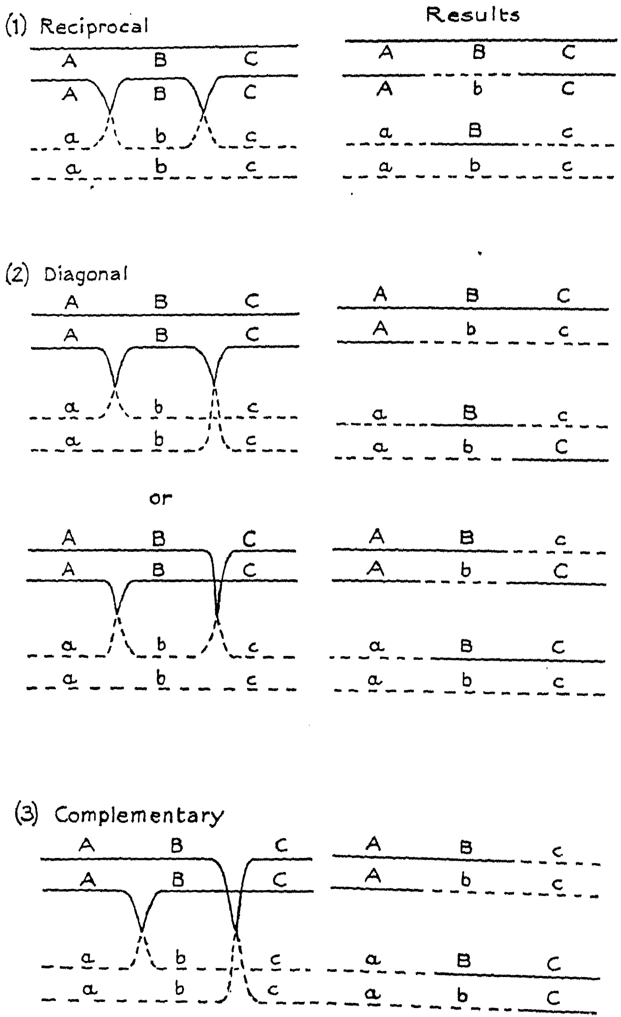


FIG. 20. For description see text, p. 89.

mentary) or one of the chromatids takes part in both chiasmata (diagonal Sansome disparate, Darlington).* There are two diagonal types corresponding to each of the two chromatids involved at the first chiasma. The diagonal type is known as non-compensating while the reciprocal and complementary types are known as compensating types, in cytology. Hearne and Huskins (1935) have been able to distinguish these types cytologically in *Melanoplus femur-rubrum*. The reciprocal type gives gametes A B C, a b c, a B c, A b C, *i.e.*, two non-cross-overs, and two double cross-overs. One diagonal type gives A B C, A b c, a B c, a b C, *i.e.*, one non-cross-over, one double cross-over and two single cross-overs. The other diagonal type gives a b c, A B c, A b C, a B C. From the complementary type we expect four single cross-overs. If all four types occur with equal frequency we expect equal proportions of 4 non-cross-overs, 4 single cross-overs in the region A B, 4 single cross-overs in the region B C, and 4 double cross-overs in A C. Present evidence indicates that these types occur on a random basis., *i.e.*, there is no *chromatid interference*. Whether chromatid interference does ever occur is doubtful (see, however, Mather (1938), Sax (1932), Hearne and Huskins (1935)). It should be noted in passing that the cross-over percentage of the distance A C of this example is $\frac{4+4}{16}=50\ \%$; distances as great or greater than 50 units long cannot normally be measured from pure linkage experiments in diploids.

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* *Note.* There are at least six sets of terms for these simple arrangements of two chiasmata.

The output of 0, 1, 2, 3, 4 chiasmata in terms of cross-overs is :—

Cross-overs

	0	1	2	3	4
Chiasmata 1	0·5	0·5			
2	0·25	0·5	0·25		
3	0·125	0·375	0·375	0·125	
4	0·0625	0·25	0·375	0·25	0·0625

For example, one chiasma gives 50% non-crossed-over and 50% single crossed-over chromatids.

The number of crossed-over chromatids resulting from 1, 2, 3, 4 chiasmata can therefore be estimated as follows : Let a, b, c, d, e be the frequencies of 0, 1, 2, 3, 4 chiasmata, and s, t, u, v, be the frequencies of recovered chromatids with 0, 1, 2, 3, cross-overs in a length of chromosome.

$$s = a + \cdot 5\,b + \cdot 25\,c + \cdot 125\,d \quad \ldots\ldots$$
$$t = \cdot 5\,b + \cdot 5\,c + \cdot 375\,d \quad \ldots\ldots$$
$$u = \cdot 25\,c + \cdot 375\,d + \cdot 375\,e \quad \ldots\ldots$$
$$v = \cdot 125\,d + \cdot 25\,e \quad \ldots\ldots$$

This may be transformed into the more useful

$$a = s - t + u - v \quad \ldots\ldots$$
$$b = 2\,t - 4\,u + 6\,v \quad \ldots\ldots$$
$$c = 4\,u - 12\,v \quad \ldots\ldots$$
$$d = 8\,v \quad \ldots\ldots$$

With these equations it is possible to analyse the massive crossing-over data from *Drosophila melanogaster* and *Zea* in terms of chiasmata with mutual advantage to geneticists and cytologists (see Weinstein (1936), Mather (1933, 1935, 1937), Charles (1938)).

Double Crossing-over

Relationship between Chiasmata. If the distance between two genes is great there is a chance for two cross-overs to take place between them. This double crossing-over or *coincidence* is therefore a function of the distance between the genes. The distance in which double crossing-over can occur has a particular value which varies with the part of the chromosome involved. Bridges and Morgan (1923) showed that the coincidence in the X-chromosome of *D. melanogaster* is greatest in the neighbourhood of *tan* where double cross-overs may occur in a section as small as 13 units. Coincidence may be as high as 1·3 and double cross-overs occur within 6 units in the middle regions of chromosome III. Double cross-overs are extremely rare in 20 units of cross-over at a distance of 15 units from the ends of the chromosomes (Morgan, Bridges and Sturtevant, 1925).

The region of the centromere in *Drosophila* has increased double crossing-over and decreased single crossing-over as compared with other regions (see Beadle, 1932). These facts may be due to the non-proportionality of the genetic and physical distances (Schweitzer, 1935), see p. 109.

If coincidence of crossing-over involving only two chromatids takes place (in the Figures 16 and 12) the resulting crossed-over chromatids will be **aBc** and **AbC**. Hence double crossing-over leaves **A C** and **ac** in the same relation to one another after meiosis as before. Therefore, in genetical results the detectable cross-over value between **A** and **C** will be less than the real value. Thus in calculating the cross-over value of **AC** from the sum of the cross-over values of **AB** and **BC** correction must be made for this fact of double crossing-over.

As Haldane (1918*a*,*b*) points out, if **AB** has the cross-over value m and **BC** has the value n in a triple heterozygote the total result of cross-overs in the different regions is :—

non-cross-overs	**ABC abc** $(1 - m)(1 - n)$
single cross-overs	**aBC Abc** $m(1 - n)$
,, ,,	**ABc abC** $n(1 - m)$
double cross-overs	**aBc AbC** mn

The value **AC** will be $m(1 - n) + n(1 - m)$, *i.e.*, $m + n - 2mn$, when double cross-overs occur and $m + n$ when no double cross-overs occur. The value $m + n - 2mn$, however, is rarely realised

TABLE 12

Three Point Tests

Backcross Data

Species.	F_1 Genotype	Parental Combinations	Recombinations.			Co-incidence	Authority.
			1	2	1 and 2		
Zea Mays .	$\frac{\mathrm{C\ sh\ +}}{\mathrm{+\ +\ wx}}$	2,538 2,708 5,246	116 113 229 3.4%	601 626 1,227 18.3%	4 2 6 0.1%	0.14	Hutchison (1922).
Primula sinensis.	♀ $\frac{\mathrm{S\ B\ G}}{\mathrm{s\ b\ g}}$	1,674 1,670 3,344	131 125 245 6.6%	715 789 1,504 32.1%	43 45 88 1.7%	0.86	de Winton & Haldane (1935).
Primula sinensis	♂ $\frac{\mathrm{S\ B\ G}}{\mathrm{s\ b\ g}}$	2,217 2,070 4,287	350 371 721 11.6%	1,264 1,139 2,403 35.0%	116 119 235 3.0%	0.77	de Winton & Haldane (1935).
Lycopersicum esculentum.	♂ $\frac{\mathrm{D\ P\ O}}{\mathrm{d\ p\ o}}$	257 159 416	78 15 2.9%	36 36 72 14.3%	— 0.0%	—	Sansome (1933.)

Under the heading " Recombinations " region 1 gives the number of cross-over plants resulting from crossing-over between the left-hand factor and the central factor, while region 2 gives the cross-ove plants resulting from crossing-over between the central factor and the factor on the right han in experiments. More usually the value lies between $m + n - mn$ and $m + n - 2mn$ in moderately large distances between **A** and **C**. One cross-over interferes with the formation of another cross-over within a certain distance from it. This interference necessarily reduces the number of double cross-overs. Hence interference is the reciprocal of coincidence, which is measured by the coefficient, observed/calculated double cross-overs. When the coincidence is 1, interference is at a minimum, while coincidence equal to zero indicates 100% interference.

The coefficient of coincidence is most easily calculated from the formula :—

$$\text{coefficient of coincidence} = \frac{xn}{ab}$$

in which x is the number of observed double cross-overs, n is the total number of plants and a and b the single cross-overs observed in regions 1 and 2 respectively, *i,e* , $\overbrace{\mathbf{A}_1 \mathbf{B}}^{a}\overbrace{{}_2\mathbf{C}}^{b}$

Stevens (1936) has analysed the usage of the co-efficient of coincidence and pointed out that it is necessary to use a particular method when calculating the co-efficient for non-adjacent regions of the chromosome. As a result, he is able to show that coincidence rises steadily to unity with increasing distances in the X-chromosome of *Drosophila,* and that the reappearance of interference to form nodal points above 40 units distance does not take place as was previously thought.

Chiasma Formation. Recent cytological work indicates that the formation of one chiasma influences the formation of another in its neighbourhood. Haldane (1931) analysed the cytological data of eight species of plants, *Vicia Faba, Matthiola incana, Campanula persicifolia, Pisum sativum, Tulipa australis, Fritillaria imperialis,* and two species of *Rosa* which had been examined by Maeda, Darlington and others. He showed that in these species the chiasma frequency per bivalent did not correspond to the Poisson series expected if the chiasmata were formed independently of one another. Instead it was found that the ends of the observed curve were truncated and that there was a considerable concentration of frequencies round the mean. Table 13 from Haldane (1931), gives the observed and calculated chiasma frequencies per bivalent in the case of the long chromosome M of *Vicia Faba* (Maeda, 1930*b*). There is a large concentration at 7–10 chiasmata in the observed frequencies. This might indicate either that the chiasma formation is localised in particular regions or that one chiasma interferes with the formation of another distal to it. Maeda, however, has shown that a chiasma may arise anywhere along the length of the chromosome and localisation does not occur.

TABLE 13

Maeda's Data for the Long Chromosome in (Vicia Faba *ex.* Haldane, 1931)

x	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
n obs.	0	0	0	1	3	7	13	33	39	41	28	8	8	0	0	0	0	0	0	0	0
n calc.	0·0	0·3	1.4	4·0	8·5	14·2	19·9	23·9	25·0	23·3	19·6	15·0	10·5	6·8	4·0	2·3	1·2	0·6	0·3	0·1	0·0

Mather (1936, 1937) shows that in *Drosophila* the chiasma proximal to the centromere is formed at a certain distance from the centromere, and that this distance varies with the length of the chromosome limb ; the longer the limb the greater is the distance of the proximal chiasma from the centromere. This variable distance determines the position on the chromosome where high crossing-over occurs (see p. 109), since Mather shows that the mean distance between the first and second proximal chiasmata ("interference distance") remains constant in the *X*, *II* and *III* chromosomes of *D. melanogaster*. Cytological evidence indicates that this relation of the centromere with the proximal chiasma is a general one. Mather suggests that the proximal chiasma is the first to be formed, and that its formation influences the formation of succeeding chiasmata. Schweitzer (1935) deduces from similar data that crossing-over may begin at random on the chromosome. Charles (1938) has also analysed genetical data in *Drosophila* and suggests that both the end of the chromosome arm and the centromere influence the position of crossing-over and that the first formed chiasma need not be proximal to the centromere. He further illustrates a useful method for obtaining the average percentage of crossing-over in each section of the chromosome. The statistical analysis of crossing-over is a valuable method for the study of chromosome behaviour during prophase, but the conclusions must be regarded critically.

Association may start anywhere on the chromosome, with a tendency to begin at the ends in *Zea* (McClintock, 1932), while Sansome, E. R. (unpub.) has shown that pairing begins usually at the ends of a structurally changed chromosome of *Pisum sativum*. Darlington (1936) shows that pairing is most frequent at the ends of the chromosomes of the structural hybrids of *Rhoeo* while Dobzansky and Tan (1936) observed this fact in *Drosophila*.

It is highly important to discover if pairing and if chiasma formation start at a particular region. The theories of the origin of differential segments in structural hybrids, of pairing, homology and disjunction would all be modified by a localisation of the commencement of either. The place of commencement of pairing, however, may or may not effect the point of commencement of chiasma formation.

Darlington had found that there was a negative correlation (– 0·330) between the frequency of chiasmata in the smallest bivalent and the frequency of chiasmata in the remaining bivalents of 8 chromosome *Secale cereale*. Mather (1936), Mather and Lamm (1935) have statistically examined a number of rye plants and numerous animal and plant species for negative correlation. They claim to have shown that frequently, but not universally, there is a definite relation between the frequency of chiasmata in one bivalent with that of others in the same cell, and Mather (1936) suggests that the bivalents "compete for chiasmata" in one nucleus. Sansome (in press) provides evidence of the difficulties met with in this type of analysis. If there is negative correlation between the chiasma frequencies of different bivalents, we expect to observe correlated genetical crossing-over in two different bivalents. Increased crossing-over in one bivalent should be accompanied by decreased crossing-over in another. de Winton and Haldane (1935) do not find this in *Primula sinensis*, but there are possible indications of it in abnormal forms of *Drosophila melanogaster* (Morgan, Bridges and Schultz (1933), Steinberg (1935)). The application of statistical methods to chromosome behaviour is a valuable means of analysis but definite genetical evidence of negative correlation will be more satisfactory since size of bivalents, presence of inversions and duplications, non-proportionality of chiasma frequencies and length, terminalisation and several other phenomena are not controllable by the analysis of variance method as used by Mather.

Mode of Crossing-over. Darlington (1935) has published a theory of crossing-over which arises from his theories on chromosome mechanics. He supposes that the four chromatids are twisted spirally round each other under strain at pachytene and that the chromatids are held tightly to each other by attraction of small parts throughout their length. Under strain, one chromatid breaks and that break induces a half twist to release tension and also induces a break, by causing extra strain, in the corresponding chromatid. A new union by attraction under no or little tension then occurs to give a chiasma. This theory to explain why chromatids break and rejoin at identical parts probably approaches fact, whether the general torsion theory is correct or not (see also Belling, 1933).

Conditions of Crossing-over. Genetical evidence is fairly complete as to the time and the manner of crossing-over during meiosis. Plough (1917, 1921) and Gowen (1929) utilised the fact that temperatures over 25° C. increase crossing-over in *Drosophila*. Females were raised in temperatures over 25° C. and at various ages were introduced into normal temperatures for egg-laying. Plough concluded that crossing-over had taken place seven to eight days before the eggs were laid, since the effect of the temperature upon egg-laying was detectable up to that period. The early stages of the first maturation division take place about seven to eight days before egg-laying. Evidence from triploid *Drosphila melanogaster* (Bridges (1916), Bridges and Anderson (1925), Morgan, L. V. (1925), Anderson (1925), Redfield (1930) and others), from trisomic maize (Rhoades, 1933), tetraploid *Lycopersicum esculentum* (Sansome, 1933), and tetraploid *Primula sinensis* (de Winton and Haldane, 1935), indicates that crossing-over takes place after the chromosomes separate into their component chromatids. The genes **pr**, $\mathbf{v}_2$ are situated on either side of the centromere of chromosome V in *Zea Mays*. They are 41 cross-over units apart and **pr** is closer to the centromere than $\mathbf{v}_2$. Rhoades (1933) crossed trisomic plants of the constitution **Pr** $\mathbf{V}_2$,

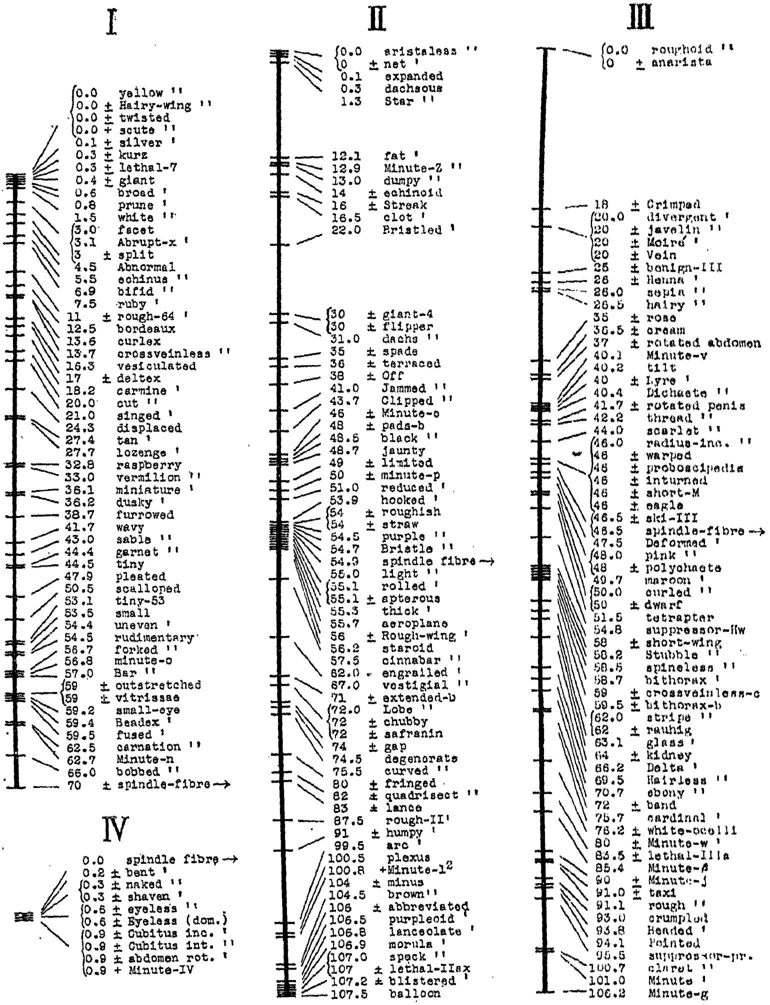

FIG. 21. Maps constructed from data kindly provided by Dr. C. B. Bridges (June, 1932), showing principal loci in chromosomes I, II, III, and IV in *Drosophila melanogaster*. The symbol '' designates the most useful types, ' those nearly as good, while those unmarked are important only in special connections.

Pr V$_2$, pr v$_2$ with the double recessive diploid **pr v$_2$, pr v$_2$**. Among the progeny were 61 plants homozygous for **v$_2$v$_2$v$_2$** and 9 plants homozygous for prprpr. Since the diploid recessive parent pr v_2, pr v_2 only supplies one pr v_2 to the progeny the trisomic parent although only containing one pr v_2 chromosome contributes two representatives to the progeny. Doubling of the genes therefore takes place before separation, *i.e.*, before meiotic metaphase I. The frequencies of homozygosity of pr (9) and v_2 (61) are different (many of the progeny were of the constitution Pr v_2, pr v_2, pr v_2). These phenomena can only be brought about by crossing-over between chromatids after splitting of the chromosomes and before disjunction at metaphase.

Parental Combination.		Chromatids.	
		Before Crossing-over.	After Crossing-over.
Chromosomes 1.	Pr V_2	Pr V_2, Pr V_2	Pr V_2, Pr v_2
,, 2.	Pr V_2	Pr V_2, Pr V_2	Pr V_2, Pr V_2
,, 3.	pr v_2	pr v_2, pr v_2	pr V_2, pr v_2

If normal disjunction took place after such crossing-over between the chromatids, there would be four types of gametes, Pr V_2, Pr v_2, pr V_2, pr v_2, resulting from chromosomes 1 and 3. If these all went to one pole at anaphase I (non-disjunction), the second division would produce $n + 1$ gametes in the proportion 1 Pr V_2 pr V_2, 1 Pr V_2 pr v_2, 1 Pr v_2 pr V_2, 1 Pr v_2 pr v_2, as contributions to form trisomic progeny. A constant feature in maize, *Primula sinensis*, *Lycopersicum esculentum* and *Drosophila* is that genes near the centromere do not show as much homozygosis as those from distant regions. Homozygosis is the frequency with which one recessive gene present in a heterozygous parent appears in the homozygous state in the progeny. Pr is near and V_2 at a greater distance from the centromere; pr shows 1·2% homozygosis and v_2 4·1% homozygosis among the trisomic progeny of the cross.

Morgan, L. V. (1925), Anderson (1925), Morgan, Sturtevant and Bridges (1933), Bridges and Anderson (1925), Redfield (1930), Beadle (1934, 1935), Beadle and Emerson (1935), Emerson and Rhoades (1933), Rhoades (1931, 1933), etc., supply important data which considerably extend our knowledge of crossing-over. At a particular region near the centromere between Bar and bobbed in the *X* chromosome of *Drosophila melanogaster*, in the middle of chromosome III between scarlet and curled (or Peach) there was a complete absence of homozygosis of the genes, whereas at greater distances from these regions, homozygosis increased in frequency. The following percentages of homozygosis in attached *X*-stocks of *Drosophila* were found by Rhoades (1931).

TABLE 14

bb	f	g^2	t	ct	rb	ec	w^a	x	
ob. 0	5·2	9·5	16·1	15·5	17·7	17·4	17·8	18·2	18·9
exp.	5·2	10·4	16·1	17·6	18·4	18·4	18·2	18·2	18·2

In these stocks two *X* chromosomes are attached together near the centromere and non-disjunction takes place regularly, therefore the observed differences must be due to crossing-over. Crossing-over between two genes will produce **AB, Ab, aB, ab** in chromatids (*cf.* Fig. 20). If **A** and **A** separate from **a** and **a** at metaphase (reductional separation), then **Bb** will separate from **Bb** (equational separation), thus $\frac{\mathbf{AB,\ Ab}}{\mathbf{aB,\ ab}}$. In other words the occurrence of one chiasma between **A** and **B** will give rise to equational separation of **B** and chromatid parts distal to it. Disjunction will produce four normal gametes **AB, Ab, aB, ab,** since the two meiotic divisions separate all four chromatids. Non-disjunction, associated generally with metaphase I, however, prevents the first separation **AB, Ab**—**aB, ab,** and combines the products in one cell. At the second division **AB** separates from **Ab** and **aB** from **ab** as in normal cases, but now **AB** is combined in one gamete with **aB** or **ab,** and **Ab** with **aB** or **ab.** The last combination is the equational exception, giving rise to homozygosis of **b** in the progeny. Therefore homozygosis depends on the occurrence of non-disjunction and equational separation. The increase in frequency of homozygosis as the distance from the centromere increases therefore indicates that (1) chromatids do not separate from one another at this point until the second division, *i.e.*, separation is always reductional at the centromere; (2) the frequency of homozygosis is proportional to the crossing-over which takes place between the centromere and the locus of the gene. Mather (1936 *b*) has developed formulæ for evaluating these variables.

Since homozygosis depends on the amount of equational separation when there is regular non-disjunction as in attached *X*s, it is necessary to discover the amount of equational separation after the formation of one, two, three or more chiasmata between the centromere and locus of the gene. Weinstein (1936), Mather (1935) have treated this subject mathematically with the following result:—

TABLE 15

No. of Chiasmata.	Proportional Equational Separation.	Homozygosis.
0	0	0
1	1	$\frac{1}{4}$
2	$\frac{1}{2}$	$\frac{1}{8}$
3	$\frac{3}{4}$	$\frac{3}{16}$
4	$\frac{5}{8}$	$\frac{1}{10}$
5	$\frac{11}{16}$	$\frac{11}{64}$

Therefore, even after 5 chiasmata, there is not random separation between a locus and the centromere. Randomness is only approached after an infinite number of intervening chiasmata.

Since in the attached *X* case only one out of the four combinations of **AB**, **Ab**, **aB**, **ab**, namely **Ab**, **ab** gives rise to homozygosis of the recessives the frequency of homozygosis is $\frac{1}{4}$ of the frequency of equational separations. Utilising this fact together with the formula of Belling, Sax and Mather for converting frequencies of crossing-over into chiasma frequencies, we can estimate the homozygosis expected in the *Drosophila* case above. Agreement is close (see Table 14) and it should be noted that homozygosis resulting from complete random separation, *i.e.*, $\frac{1}{4}$ of $\frac{2}{3}$ or 16·7% is not observed even at the distal end of the *X* chromosome. An extension of these methods to tetraploids may be made (Sansome, 1933, Mather, 1936) where chromatid segregation (Sansome, 1933), also depends on the production of equational exceptions by equational separation, accompanying non-disjunction. Qualitative proofs similar to **pr**, $\mathbf{v_2}$ in maize are available in tetraploid *Primula sinensis* (de Winton and Haldane, 1935), *Datura Stramonium* (Belling, Blakeslee and Farnham, 1923), and *Lycopersicum esculentum* (Sansome, unpub.). In these cases either plants of the constitution **AAAa** have given **aaaa** progeny, or **Aaaa** plants have given **AAaa** progeny when crossed to the recessive (see p. 181).

Crossing-over in Fungi. Lindegren (1936) makes use of the phenomenon of equational separation to construct a linkage map of *Neurospora crassa* where the line of 8 spores in the ascus reflects the divisions antecedent to its formation (see Fig. 12).

The analysis of tetrads of spores in other organisms (see pp. 16, 49) shows that segregation takes place either at the first or second division of meiosis. Since the chromosome does not divide at the centromere, until the end of the first division, it is possible to account for the general phenomena. All genes close to the centromere will exhibit segregation at the first division (reductional separation) and genes at increasing distances from the centromere will segregate at the second (equational separation) as well as at the first division, in a frequency proportional to the frequency of chiasma formation, which depends on the distance from the centromere. The occurrence of chiasmata will permit equational separation of the genes at the first division. For example, the segregation of + and −, Gap **G** and non-gap **g** was studied in one cross. The parental combinations +**G**−**g** were recovered 634 times and the recombinations −**G**+**g** were found 58 times. The cross-over percentage therefore is $\frac{58}{692} = 8{\cdot}4\%$. **G** separated from **g** 165 times at the first division and 23 times at the second division, *i.e.*, $\frac{23}{188} = 12{\cdot}2\%$ equational separation $= 6{\cdot}1\%$ crossed-over chromatids. The ± pair of allelomorphs separated 142 times at the first division and 36 times at the second division, *i.e.*, 20·2% equational separation = 10·1% crossed-over chromatids. Hence the order of the genes and the centromere ↑ on the chromosome is + 8·4 **G** 6·1 ↑ . The distance **G**—— ↑ will include double cross-overs which naturally cause a reduction in the observed crossing-over (10·1%). By observing the arrangement of the spores it is possible to distinguish double cross-over types from non-cross-overs. When these are allowed for, the distance +—↑ becomes 14·6, a very close agreement with the sum of 6·1 and 8·4. The genes "crisp," "pale," and "dirty" were located on the other arm of this chromosome with the median attachment. Somewhat analogous results are reported by Wettstein (1924), in mosses, Allen (1930), in *Sphaerocarpos*, and Michaelis (1931), in *Epilobium*.

Bridges and Anderson (1935), working on the *X*-chromosome, and Redfield (1930) on the II. and III. chromosomes of *Drosophila melanogaster*, raised triploids in which all three homologous chromosomes were marked throughout their length by genes. The history of the parts of the chromosomes could therefore be followed and hence the gametic output in terms of the *X*, II, or III chromosome could be compared with the parental constitution. It was found, for example, that one resultant chromosome was composed of parts of three original chromosomes indicating that crossing-over between two of the three chromosomes at one point could be accompanied by crossing-over between a third chromosome and one of the participants at a different point. These *progressive* double cross-overs equal the number of *recurrent* double cross-overs in which only two chromosomes are involved, Therefore, crossing-over between any two homologous chromosomes in the triploid *Drosophila* does not interefere with crossing-over with a third chromosome in a different region. Mather (1933) however has shown that this is only partly true; since the pairing of parts of two chromosomes influences to some extent the pairing of neighbouring parts. A further proof that crossing-over takes place after the separation of chromatids is that the six strands in a trisome may all be different from one another in gene content after crossing-over.

Proof from the same work was obtained that (1) crossing-over may take place between any two chromatids which are not derived from the same chromosome, *i.e.*, **AB**, **AC**, **BC**, but not **AA**, **BB**, **CC**; (2) chromatids derived from the same chromosome remain associated at the centromere until the end of the first division of meiosis. Evidence that chromatids derived from one chromosome do not cross-over is obtained from (1) Sturtevant's work (1925, 1928) (see p. 127) on Bar eye: (2) L. V. Morgan's work (1933) on the ring *X* chromosomes in *Drosophila*: (3) Weinstein's mathematical analysis of crossing-over in *Drosophila melanogaster* (1936).

GENETICAL AND CYTOLOGICAL LOCI

The locus of the centromere has been genetically determined in several chromosomes of Maize and species of *Drosophila*, and has been indicated in *Primula sinensis*, *Neurospora crassa* and other plant species. The region is characterised by :—

(1) An absence of equational separation of genes.

(2) High coincidence and low crossing-over.

(3) Crossing-over more greatly affected by differences of temperature, age and other environmental influences (Stern, 1926 *c*, Bridges and Morgan, 1919).

(4) The presence of an inert region close to the centromere. This is proved in *Drosophila* species, and indicated in *Zea*, *Tradescantia*, *Fritillaria*, *Lycopersicum*, *Crepis*, and other plants (see p. 106, and Darlington, 1937, p. 330).

A striking confirmation that genes are linearly arranged on the chromosomes is afforded by the experiments of a group of workers who utilise *X*-rays to increase the proportion of chromosomal irregularities: Stern (1926*b*, 1928, 1929*a*, 1931), Müller (1929, 1930, 1935), Dobzhansky (1929, 1930 *a*,*c*, 1931 *a*,*b*, 1932, 1933, 1938), Grüneberg (1937), Glass (1935), Painter and Stone (1935), Beadle (1932) *et al.* on *Drosophila*; McClintock (1931, 1933), Burnham (1932), Anderson (1935), Rhoades (1933) on *Zea*.

A section of a chromosome may break off the main body of the chromosome—*fragmentation.* It may become attached to a different chromosome or to a different part of the original chromosome—*translocation.* Exchange of material between two non-homologous chromosome parts may occur—segmental interchange (*reciprocal translocation*). Reduplication of parts in a nucleus such as occurs when a portion of the *X*-chromosome translocated to chromosome IV is present in the same nucleus as two normal *X*-chromosomes or deficiency may follow translocation, fragmentation, or segmental interchange. Inversion, where a part of the chromosome is inserted in a reverse order to the original position also leads to the production of peculiar secondary abnormalities, which can be followed by genetical and cytological means (*Zea*, McClintock (1931), Brink and Cooper (1932), Creighton and McClintock (1931), Creighton (1934) ; *Trillium*, Smith (1935) ; *Drosophila*, Sturtevant and Beadle (1936) ; *Matthiola*, Philp and Huskins (1931) ; and pp. 252, 262). These abnormal chromosome arrangements necessarily lead to certain definite genetical results which give valuable information on points which cannot be easily obtained from material with a more normal chromosome behaviour.

Linkage studies (Anderson (1925), etc.) had shown that a recessive factor " bobbed " which determined the length of hair in *Drosophila melanogaster* was situated on the *X* chromosome near the centromere. Bobbed is only expressed in the female and does not appear in the male although it may be homozygous. Stern (1926 *a,b*) showed that there was an inhibitor carried by the *Y* chromosome which prevented the expression of bobbed in the male. This conclusion was based on the following grounds :—

(1) Through primary non-disjunction, males of the formula *XO* can be obtained. If the recessive **bb** is present they show the characteristic bobbed hairs.

(2) *XXY* females which are homozygous for bobbed do not show the bobbed character while their normal *XX* sisters do.

(3) Gynandromorphs which have no *Y* chromosome show the bobbed character on both the male *XO* and female *XX* sides of the body.

Experiments showed that this inhibitor was not linked to any factors on chromosomes *X*, II, III and IV. This supports the view that the inhibitor is on the *Y* chromosome. Generally, the inhibitor and bobbed were independent, but Stern found that in the progeny from a cross, bobbed female $X(\mathbf{bb})\ X(\mathbf{bb}) \times X(\mathbf{bb})Y^{\mathrm{Ibb}}$, there were no bobbed daughters. It was found on cytological examination that the *X* chromosome was joined to the *Y* chromosome at one end—the attachment end. These non-bobbed daughters therefore had received the *Y* chromosome containing the inhibitor along with the *X* chromosome from their father. Further genetical experiments showed that the inhibitor and **bb** were behaving as if closely linked. It was therefore suggested that the inhibitor must have been on the longer arm of the *Y* chromosome which was joined to the *X*, and that both **bb** and the inhibitor were not far from the point of attachment to the spindle fibre and from each other. By further experiments, Stern (1926*a*, 1927*a*) showed cytologically that bobbed and the inhibitor were indeed in the regions suggested by the genetical results. Material was obtained in which, as the result of fragmentation, different lengths of the *Y* chromosome were present in a nucleus with the *X* chromosome containing **bb**. The expression of **bb** was only inhibited when the portion of the long arm of the *Y* chromosome nearest the spindle fibre attachment was also present. When that portion was absent and any other portion of the *Y* chromosome was present, the flies were bobbed.

During Stern's work it was found that both distal portions as K_1 and K_2 of the *Y* chromosome carried material which was necessary for the fertility of the male *Drosophila*. Previously it was known that the *Y* chromosome did not carry identifiable factors but that it was essential for the fertility of the male. Stern's work showed cytologically that two definite portions of the *Y* chromosome, and not the whole chromosome, controlled fertility.

Muller and Painter (1929), Painter and Muller (1929), Dobzhansky (1929, 1930 *a,c*, 1931 *a,b*), studied the translocations of the II, III and *X* chromosomes to other chromosomes. The change in chromosome structure may be observed cytologically and the genes involved can be identified by breeding. Thus, where a small translocation from one end of the third chromosome to the fourth chromosome is observed cytologically, it is found that only those genes are involved which were believed from genetical work to be located in that region. Larger translocations have progressively greater numbers of genes. Incidentally the translocation to the fourth chromosome will change the linkage relationships by bringing the genes of the fourth chromosome and those in the translocation into one linkage group. A cytological map may be formed by noting the size of the translocation and the particular genes contained in it. Comparison therefore can be made between the genetical linkage maps from diploid and triploid data, and the cytological maps from mitotic chromosomes in *Drosophila* (see Fig. 22).

Salivary gland chromosomes. A further important means of analysis is afforded by the examination of the salivary-gland chromosomes (polytene chromosomes). The cells of the salivary glands of various larvæ of the *Diptera, Hymenoptera,* and *Neuroptera* are greatly enlarged and contain chromosome structures which are enormously enlarged (150 times the length; 400–1,000 times the volume of normal mitotic chromosomes) (Metz and Lawrence, (1937), Metz (1935)). The nature of the structures is a matter of theory (see Bauer (1936), Heitz (1933), Koltzoff (1934), Muller and Prokovieva (1935)), but the characteristic appearance of bands or discs separated by achromatic material is of great value to the geneticist (Bridges (1935, 1938), Painter (1935), Koller (1934)). Each part of the chromosome of *Drosophila* species has a characteristic number and position of the bands and therefore may be recognised (Bridges, 1938). Further, close pairing of homologous parts of the chromosomes takes place so that any differences between the chromosomes may be detected. Again, the centromere region is characterised by a less organised material (heterochromatin) —the so-called " inert region."

Several characteristics of this region have genetical importance.

(1) The heterochromatin is of two types α and β heterochromatin (Heitz, 1933).

(2) β Heterochromatin at least contains genes rather widely spaced. The *Y*-chromosome once believed to be devoid of genes has β-heterochromatin in a position corresponding to that of the *X*-chromosome (Muller and Gershenson, 1935).

(3) Breaks occur in the β-heterochromatin much more frequently than in the rest of the chromosome (Muller and Gershenson, 1935).

(4) Few gene mutations occur in β-heterochromatin.

The heterochromatin of otherwise non-homologous chromosomes appears to be homologous. In the " chromocentre " all the " inert " regions of the *X*, II, III, and IV amalgamate (Prokovieva-Belgovskaya, 1935). Thus there is support for the genetical surmise (Sansome, 1933) that the centromere regions of non-homologous chromosomes are similar and homologous. Pairing at zygotene and chiasma formation may be initiated by this close association of the centromere regions (Painter, 1935).

The analysis of salivary gland chromosomes enables one (1) to identify the parts of a chromosome involved in any chromosome rearrangement (Koller (1936), Tan (1935), Grüneberg (1937)) : (2) to detect deficiencies and duplications of small size

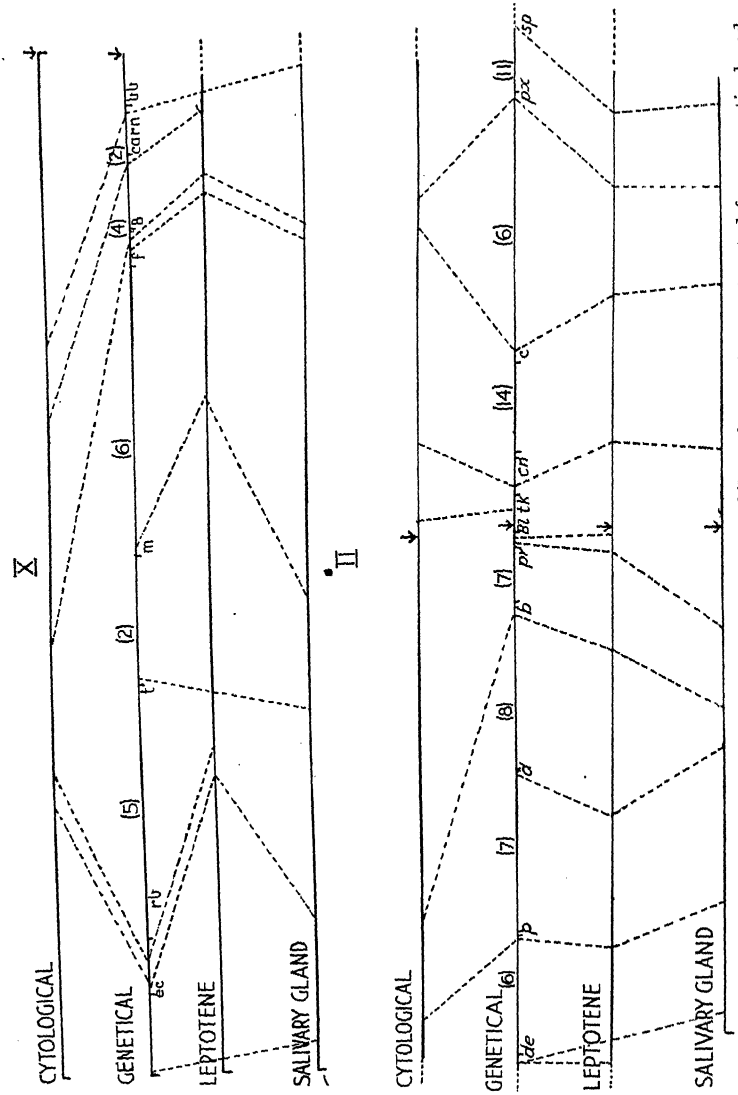

FIG. 22. Map of the *X* and II chromosomes of *Drosophila melanogaster* constructed from genetical and cytological data; see text for explanation.

and to show that small duplications are of great importance in speciation (Bridges (1935), Müller (1935)): (3) to compare the chromosome of *Drosophila* species (see Dobzhansky, 1938) : (4) to obtain an accurate map of the location of genes on the chromosome.

Chromosome Maps. Fig. 22 compares the genetical maps from diploid and from mutation data and the cytological maps from normal mitosis and from salivary glands of genes in *Drosophila melanogaster*. Several striking and important differences are observed between them. In the genetical linkage maps the distances between the genes near the centromere are shortened while those in distal regions are slightly lengthened as compared with the cytological maps ; in regions near the centromere crossing-over per unit cytological distance is much less than it is in distal regions. The triploid genetical map is intermediate in this respect between the diploid genetical and the cytological maps. The salivary gland chromosomes show that inert regions are localised round each of the centromeres. The different sizes of the inert regions considerably influence segregation. Beadle has shown that if the right limb of chromosome III at curled is broken and translocated to the small IV chromosome, then crossing-over in the region **cu-sr** is much reduced as compared with normal. In other words, by placing the centromere (in the III–IV translocation) closer to **cu-sr** than in normal chromosomes, the crossing-over is reduced. The inert region of the *X*-chromosome occupies at least half of the normal mitotic chromosome, whereas the inert regions of the II, III, and IV are much smaller, although of appreciable size. Grüneberg (1937) has shown that there are at least 5 cross-over units between bobbed (**bb**), known to be in the inert region and the centromere on the *X* chromosome. Breaks as a result of *X*-rays are more frequent in the inert region, possibly because the chromosome is less coiled in this region (see Muller and Gershenson (1935), Painter (1935)).

It is necessary to point out that crossing-over occurs at prophase of meiosis while the cytological maps are from mitotic and polytene chromosomes. The possible occurrence of differential stretching and condensation of the chromosome may somewhat distort the relationships between the maps. Schweitzer has constructed " leptotene " maps of *Drosophila melanogaster* by placing each gene on the map by the percentage of genes which are found to the left and right of its locus. " Cut," for example, is placed at

50 since half the genes of the *X*-chromosome lie on its right and half on its left. These leptotene maps approach the "cytological" maps given in Fig. 22, but Schweitzer's more accurate figures should be used in research work. The important work of Muller and Prokovieva-Belgovskaya, Painter and his workers in identifying changes in particular bands of the salivary chromosomes with gene changes should be noted.

The effect of translocation upon crossing-over in the broken chromosome is of importance. It is found that when a breakage occurs to the right of the factor for purple on the second chromosome the crossing-over in all regions to the right is decreased, but to the left it is normal. Similarly, if the breakage occurs to the left of purple the crossing-over in all regions to the left is decreased, while to the right of purple the cross-over values are equal to or slightly above normal. The same phenomenon is observed in the third chromosome. The factor scarlet in the latter case is nearest the point at which the change in the cross-over value due to the effect of translocation takes place. The factor purple and the factor scarlet are situated near the centromere in the second and third chromosomes respectively. The following table by Dobzhansky (1929*a*) illustrates the abrupt change in cross-over values as compared with normal in the different translocations. Translocations a, b and c involve one side of the third chromosome, while c and d involve the other arm.

A reasonable explanation of this phenomenon may be put forward in terms of the chiasmatype theory. If homologous chromomeres pair, one expects that the whole chromosomes will only pair normally if the linear arrangement of these homologous chromomeres is the same in both chromosomes. This order will be upset by translocation, inverson or duplication, and both the part affected and neighbouring portions of the chromosome will behave abnormally. Hence chiasma formation and crossing-over will be influenced greatly by the presence of non-homologous segments in apposition to one another on the pairing chromosomes.

Dobzhansky (1931*a*) arrives at a very similar conclusion from genetical lines of approach.

Dobzhansky (1932, 1933, 1934) and other *Drosophila* workers have genetically investigated the relations of pairing, crossing-over

TABLE 16

The Standard Values of crossing-over between the Genes of the third Chromosome, and the differences between Standard Values and Values observed in the Strains carrying Translocations.

(Dobzhansky, 1929*a*)

Intervals.	Standard Values.	Translocation Strains.				
		a.	b.	c.	d.	e.
ru—h	23·8	− 6·6	−2·6	+ 3·1	+ 5·2	−4·3
h—D	13·6	−10·7	−7·7	+ 1·8	+ 1·3	−2·0
D—th	1·1	− 0·9	−0·9	+ 0·4	0·0	+0·1
th—st	0·8	− 0·6	−0·5	+ 0·1	+ 0·1	−0·3
st—cu	8·1	− 1·5	−3·4	− 3·6	− 2·2	−3·0
cu—sr	15·4	+ 1·2	+1·7	−11·7	− 2·8	+0·3
sr—e^s	10·3	+ 1·4	+0·3	− 2·8	− 1·4	+1·3
e^s—*ca*	31·0	0·0	+0·1	− 2·1	−11·8	0·0

and non-disjunction of chromosomes. They show that (1) chromosomes will pair in twos and cross-over if the linear arrangement of homologous parts are the same ; (2) the presence of chromosome inversions, duplications, and translocations will interfere with pairing in their neighbourhood and the following crossing-over will be reduced ; (3) non-disjunction of chromosomes is negatively correlated with crossing-over, *i.e.*, the formation of a chiasma implying previous pairing induces regular disjunction, whereas the absence of a chiasma allows random distribution of chromosomes (formation of univalents) at meiotic metaphase (see p. 15).

Variation in Crossing-over. Variation in cross-over values is of common occurrence. A difference of 2 to 3% in crossing-over is often observable between the male and female sides of one plant (*Pisum, Zea, Primula sinensis*). The genes **S**, **B**, **G**, **L**, in *Primula sinensis* show a curious phenomenon. Although these genes are on one chromosome, the cross-over value between **S** and **B** is lower on the male side than on the female side, while the reverse is the case between **G** and **L**. The centromere is shown to be near **S** and **B** (de Winton and Haldane, 1935). The genes **V**, **St**, and **B** in *Pisum sativum* show a similar behaviour (de Winton, 1928). Differences in crossing-over values are often found between different cultures of a species (*Zea*, Collins (1924) Stadler (1926); *Pharbitis Nil*, Imai (1929); *Papaver Rhoeas*, Philp (1933)).

Changes in linkage values may be due to (1) genetic, (2) structural, or (3) environmental causes. The genetic constitution of the male *Drosophila melanogaster* very considerably reduces crossing-over in this sex (Philip (1935), Friesen (1934)). Chino and Kikkiwa (1933) found that the *X*-chromosomes and autosomes in *D. virilis* and *D. melanogaster* show similar size relationships, but that in *D. virilis* the *X*-chromosome has 182 cross-over units, and in *D. melanogaster* it has 66. There is greater crossing-over per unit length in one species as compared with another. This point should always be remembered in analysing crossing-over phenomena, even in one species. Beadle (1931, 1932, 1933) reports several cases of genes affecting meiotic behaviour. The crossing-over values are not greatly reduced although chiasma formation is much reduced. This arises from the fact that viable gametes are restricted mainly to those which arise from normal bivalent formation, which imply previous chiasma-formation.

Environmental influences, such as temperature, age of parent, are known to influence crossing-over in *Drosophila*. *Lathyrus* among plants exhibits seasonal variation in crossing-over, while crossing-over in *Lycopersicum esculentum* is slightly lower in Great Britain than in America (*e.g.*, **d-p** 3·2% as compared with 5·7% ∓ 1%). Nitrogen supply affects crossing-over in *Ustilago Kolleri* (Dickenson, 1931).

It has recently been found that high temperatures (31° C.) or röntgen radiation induces crossing-over in the male *Drosophila melanogaster*, especially near the centromeres in Chromosomes II and III (Friesen (1934), Philip (1935) *et al.*). This discovery has several important implications in relation to cytological data, genotypical control and environmental influences (see Darlington (1937), p. 370). Crossing-over in this case may not occur at the normal stage of sperm-formation.

Structural differences such as inversions or translocations may partially or totally inhibit crossing-over in the arm of the chromosome where they occur. This may be usefully applied in breeding *Drosophila melanogaster*. After synthesising a race containing several genes in the left arm of the III-chromosome of *Drosophila*, the constitution may be retained by introducing an inversion (cross-over reducer) on the homologous chromosome.

The phenomenon of crossing-over is a central part of modern genetics. On the one hand it is dependent on chromosome behaviour which is controlled by diverse influences and on the other hand crossing-over influences segregation, not only in regard to linkage in the diploid, but with greater effect in polyploids and structural hybrids. A review of recent work on crossing-over is given by Mather (1938) and Eloff (1932), while Dobzhansky (1937) gives a clear account of the phenomenon in *Drosophila*.

CHAPTER III

THE CONSTITUTION OF THE GENE

Presence and Absence Theory—Mutable Genes—Somatic Crossing-over—Mosaicism — Position Effect — Step Allelomorphism — Size of the Gene — Effects of X-rays—Dominance.

Presence and Absence Hypothesis. Mendel supposed that there was one factor for each of the characters that he studied and that each allelomorph was a distinct entity. He made no attempt to discover the relationship between two allelomorphs. Mendelian workers soon turned their attention to the elucidation of the nature of the factor and the relationship of the allelomorphs.

One of the first theories suggested was the presence and absence theory of Bateson and Punnett (Bateson, 1930). At the first enunciation, it was supposed that an organism which exhibited a dominant character possessed a factor which was absent in the organism exhibiting the recessive and alternative character.

Later it was found that more than one factor could be allelomorphic to a dominant factor. For example, there is a multiple allelomorphic series controlling the size of the eye of the flower of *Primula sinensis*. There are three factors all allelomorphic to one another. The factor Q for normal eye is dominant to a factor q for large eye, called Primrose Queen, after the variety in which it appeared, and both Q and q are recessive to Q_1 a factor for no eye (Queen Alexandra). When Primrose Queen (qq) is crossed to normal-eyed plants, the F_2 segregates into 3 normal : 1 Primrose Queen in respect to eye type. The cross, Queen Alexandra × Primrose Queen, segregates in the F_2 in the ratio 1 Queen Alexandra : 2 with intermediate eyes similar to the F_1 (Q_1q) : 1 Primrose Queen. There is no appearance of normal eyes as would be expected if normal were in a different locus. The third cross, normal × Queen Alexandra, segregates in the ratio 1 Queen Alexandra : 2 intermediate eyes Q_1Q : 1 normal with no Primrose Queen eyes appearing.

Johannsen (1923) and Morgan (1919) suggested that the theory of presence and absence was upset by the occurrence of more than two allelomorphs at one locus. Morgan pointed out in his argument that there could not be two absences corresponding to one presence. As Bateson (1926) states, however, this assumes that the recessive contains no factor at all to correspond with the presence of one in the dominant, whereas it is more probable that only a part of the dominant factor is absent in the recessive factor.

In the example quoted above, if $\mathbf{A}_1$ represents the top dominant of the series (Queen Alexandra eye) which acts as an inhibitor of the eye, normal eye could be mathematically represented as $\mathbf{A}_1 - \frac{1}{4}$ and Primrose Queen as $\mathbf{A}_1 - \frac{1}{2}$. The figures are purely hypothetical and are obtained from the relative expression of the factors $\mathbf{A}_1$, **A** and **a**. It is not known if expression is a linear function of factor content.

Several allelomorphic series, such as that which governs the structure of the flower in *Antirrhinum majus*, or the eye-colour and wing shape in *Drosophila melanogaster*, might well be composed of factors which are similar in kind but different in quantity.

The presence and absence theory thus assumes a quantitative difference between the dominant and recessive allelomorphs. It will be seen later that several recent theories of the nature of the gene are similar in some respects. It seems necessary to assume that there is also a qualitative difference between the dominant and recessive factors.

P. Hertwig (1926) studied the "**def.**" series of multiple allelomorphs of *Antirrhinum*. "**Def.**" is normal, **def. chl.** (chlorantha, Schick and Kuckuck) has light green flowers with under-developed upper and lower corolla lips, **def. nic.** (nicotianoides, Schick and Kuckuck) has a very short corolla and petaloid stamens while the extreme **def. gli.** (globifera, Schick and Kuckuck) has much reduced floral parts and deformed gynœcium with sometimes as many as six styles.

The series in order of dominance is, normal-chlorantha-nicotianoides-globifera, with normal completely dominant over all the others. The heterozygote **chlor.-nic.** is similar to chlorantha, but can be distinguished from it. **Chlor.-gli.** is intermediate between chlorantha and globifera, while **nic.-gli.** is closer to nicotianoides than to globifera. In this series, both dominance of one factor over another with respect to the principal character expression and the graded increase in abnormality, as we pass down the series, might well be obtained from a quantitative difference between the factors.

Agol (1931) has pointed out that the series of factors controlling wing shape in *Drosophila melanogaster*, namely, normal, nick, antlered, strap and vestigial, might also be regarded as differing from one another on a quantitative basis. Here the homozygous nick and normal flies cannot be distinguished phenotypically, but normal is completely dominant to vestigial, whereas nick is not. Therefore the heterozygous forms (+ **v**) and (nick-vestigial) are distinguishable.

Among other series of multiple allelomorphs which show a graded difference in expression of characters is the triple allelomorphic series **Gr**, **G**, **g** in *Phaseolus* (Emerson, 1909 and Tjebbes, 1931). Here the recessive factor **g** gives plants with yellow pods and foliage, the top dominant **Gr** gives green pods and foliage, while the intermediate factor **G** gives yellow pods and green foliage. Again there are four factors in a multiple allelomorphic series which control the distribution of pigment in the seed coat of the Soya bean (Owen (1928*b*) and Nagai and Saito (1924)).

Whether multiple allelomorphic series of factors in other plants exhibit quantitative differences in expression is as yet difficult to determine. The character which is influenced by the allelomorphic series may be one of a structural or physiological nature. Until the train of actions between the factor, as origin, and the character expression, as product, is more fully known, it is unwise to speculate as to the differences between the nature of the factors on the basis of differences between the expressions of two factors.

Imai (1931*a*,*b*) enumerates seven different series of multiple allelomorphs in *Pharbitis Nil.* The factors in each series are arranged below in the order of dominance.

(1) Normal, maple, willow (shape of cotyledon and leaf, split flower).
(2) Normal, smeary, faded (flower pattern).
(3) Normal, contracted, star (contraction of organs, flower shape).
(4) Normal, yellow inconstant, yellow (foliage colour).
(5) Normal, crepe, reversed (constitution of leaf).
(6) Margin reduced, normal, margin slight (margin of corolla).
(7) Normal, feathered, creased (crumpling of leaf and feathering of corolla).

In *Pisum sativum* Tedin (1925) indicates that in the presence of **A**, a factor for flower colour, leaf axil spot is controlled by three factors, **Dw**, **D** and **d**. **DwA** gives a double ring, **DA** a single ring, and **dA** and all **D** factors with **a** give no ring of colour in the leaf axil.

Both in maize and *Drosophila* multiple allelomorphic series with many members are known. Emerson (1914, 1917, 1918, 1921*b*), in maize, for example, found that the factor **R**, which is one of the complementary factors for plant, pericarp, and aleurone colours, was a member of the multiple allelomorphic series $\mathbf{R}_r$, $\mathbf{R}_g$, $\mathbf{r}_r$, $\mathbf{r}_g$, $\mathbf{r}_{ch}$, $\mathbf{r}_{rg}$ (see p. 78), and also that the factors **B**, $\mathbf{B}_w$ and **b**, which modify the expression of certain plant colours such as sun-red formed another series.

TABLE 17

Anderson (1924)

Factors.	Pericarp colour.	Cob colour.
RR	red	red
OR	light red to orange	red to orange
WR	white to pale orange	red
OW	light orange	white
CW	red or orange, white capped	white
CR	red or orange, white capped	red
WW	white	white
VV	variegated	variegated
MO	variegated, crown patch	light to white

Emerson (1917) studied several pericarp colours in maize and found that each depended on a factor which was not inherited independently, but which showed complete linkage. These were further studied by Anderson and Emerson (1923) and Anderson (1924), who found that they formed a multiple allelomorphic series. Table 17 illustrates the phenotypic effect of the factors. Anderson found that any factor which determined colour was dominant to factors which determined colourless pericarp, and those which gave darker colours were dominant to those determining lighter colours. Red and variegated were completely dominant to white, but $\mathbf{P}_{or}$

P_{ow}, P_{cr} and P_{cw} gave intermediate colours when combined with white, although the distribution of colour was similar to that in the coloured parent.

Anderson points out that many more factors in this series can be isolated, since subdivisions of each colour class can be made. Emerson had shown that variegated **VV** could be divided into light, medium and heavy variegation, while Hayes (1917) showed a similar series for mosaic. These mutable types are unique in that they can quickly produce a completely graded series of multiple allelomorphs.

Emerson (1914, 1917) suggested that variegated pericarp in maize was due to mutations in the pericarp colour factor during the course of the plant's ontogeny, and found that changes from variegated **V** to self-colour **S** were reversible, but with different frequencies. He also showed that only one of the factors mutated at a given time in homozygous material. In heterozygous material, where colourless pericarp was present along with either **V** or **S**, the colourless pericarp factor did not mutate.

Eyster (1924*d*, 1925) studied plants which contained the factors **ow** and **ww**, *i.e.*, they were heterozygous for orange pericarp—white cob, and white pericarp—white cob (note here that it is preferable to designate the factors thus since they have not been definitely proved to be members of the above allelomorphic series of **P** factors, although there is a strong presumption that this is the case). A complete range of colours from colourless to cherry-red pericarps was found on plants of the constitution (**ow ww**). Mutations from orange pericarp to red and to white with the consequent variegated patterns were therefore observable. If seeds with a light coloured pericarp were planted, the resultant progeny still consisted of a range from the lightest to the darkest colours. In all cases, however, the mode of the colours of the ears of the progeny approached that of the parent ear. It was found that orange seeds taken from an ear having both orange and red seeds produced plants with various shades of orange pericarp while the red seeds gave plants with red ears. The orange pericarp colour persists until late in the development and then may break up into the components red and white. This change is the most frequent (13 per 1,000 seeds), while the change from orange to red takes place less frequently (10 in 1,000). Those with heavy variegations (where the colours are intense and in large patches) are unstable and give rise to light variegations (8 in 1,000).

The variegated colour forms which resulted from the breaking up of the orange pericarp into the constituents red and white were all heritable. As in those seeds with orange pericarp each colour form tended to reproduce itself, the mode of the colour range of the progeny from a particular ear corresponding with the type of variegation of that ear. Mosaic pattern, another of the factors in this P series, was also found to behave in a similar manner. Mosaic pattern results from the juxtaposition of red and white tissue in the pericarp.

Another range of colours, including variegations, in *Verbena*, was reported by Eyster (1928). This formed an orthogenetic series similar to that of orange pericarp—colourless in maize. Here, however, dilute colour was dominant over more intense colour. The various series were thought by Eyster to have had a quantitative basis for their variation.

Mutable Genes. Among the factors which are members of a multiple allelomorphic series, there are several which mutate with a definite frequency to another member of the series, or to a state, which is distinguishable from that of another allelomorph. Generally, the mutation is in the direction of the wild type allelomorph, which is commonly, but not always, the top dominant of the series. Such mutable genes have been found in maize and Verbena and in

Antirrhinum, Baur (1924), Hertwig (1926).
Dahlia variabilis, Lawrence and Scott-Moncrieff (1935).
Delphinium ajacis, Demerec (1928).
Primula sinensis, de Winton and Haldane (1933).
Pharbitis Nil, Imai (1931*a*,*b*).
Drosophila virilis, Demerec (1927, 1928, 1931).
Drosophila melanogaster, Patterson (1930) (see Stern, 1936).

Three cases in *Drosophila virilis* and two in *Delphinium* have been more intensively studied by Demerec (1927, 1928, 1931) in order to discover the nature of mutable genes. He suggests that gene mutation is more in the nature of a chemical change than of a reassortment of physical particles.

Numerous other examples of genic mutability such as the flaking gene of *Primula sinensis*, yellow inconstant (Imai, 1929), cream (Imai, 1929) and flecked (Imai, 1931*a*,*b*) in *Pharbitis Nil* agree in that the mutability rate does not vary greatly from one generation to another and that the mutation is from the recessive to the normal dominant type. The mutation rate is low, ranging from about 0·2% in *P. sinensis* flake to 3·7% in flecked *Pharbitis Nil.*

In several cases these mutable genes have stable allelomorphs whose effects cannot be distinguished phenotypically from those of the unstable genes. Examples of such genes are reddish, miniature and magenta in *Drosophila virilis*, yellow constant in *Pharbitis* and two peculiar cases reported by Imai in *Plantago* and *Celosia*. In these two latter examples, an unstable normal type mutates to the aberrant recessive, while another normal type does not mutate.

It has been found on treatment with X-rays that certain loci of *D. melanogaster* give more visible mutants than others (Muller (1928) and Patterson (1929, etc.). These loci, such as scute, forked, and eye colour, exhibit several allelomorphs. It would appear that certain loci have more mutable genes than others at a given stage in the life history of the organism.

Sax (1931) drew attention to the fact that parts of the *X*-chromosome of *D. melanogaster* which show increased crossing-over per unit distance contain more gene mutations than other portions. Bridges (1937) has shown that there is no correlation between crossing-over and mutation rate at the right end of the II chromosome (*cf.* Schweitzer, 1935). These workers are considering visible mutations which Demerec (1937) has shown to be generally distinct in origin from lethal mutations, which, to a very large extent, are deficiencies or are associated with structural changes. Elsewhere we will show that phenomena previously attributed to gene mutation often result from somatic crossing-over, or structural abnormalities. Therefore attempts to understand the nature of the gene from the character expression must be viewed with scepticism.

Rhoades (1938) has shown that **a** mutates to **A** and $\mathbf{a^p}$ in Maize in the presence of **Dt**, but is stable in the presence of **dt**. These genes are not linked. He therefore concludes that there does not appear to be any fundamental difference between mutable and stable genes.

In *Delphinium ajacis*, rose-α, which is a factor for flower colour, mutates frequently to its purple wild type allelomorph. From seed of a selfed rose-α parent, variegated plants are obtained, in addition to a few purple and a few rose variegated and purple chimærical plants.

Purple plants arise through the reversion of rose-α to purple in the germ cells. Chimærical rose purple plants are the result of somatic reversion which has occurred early in ontogeny. It is noticeable that when a purple spot occurs on a rose-α plant it consists of one or more purple cells, surrounded by distinctly lighter purple cells. This may be due to diffusion of the pigment from the mutated cells. The stock had been started with one heterozygous plant with the lilac and rose-α genes as the allelomorphs. Since only rose-α mutates, Demerec in his study virtually followed the descendants of one rose-α gene. From such a plant the number of mutations of the rose-α gene to purple was about 1,182 per 100 sq. cm. of somatic tissue. Demerec showed that the mutation rate was the same in gametogenesis and somatogenesis and remained constant through four sexual generations.

Lavender-α mutates to purple in a strikingly different manner. It has a high rate to mutation in the early stages of development of the plant and is stable, or shows little mutability, in the early stages of petal and sepal formation, with a return to high mutability in the last stages of development.

Since the mutant cells and tissue are well defined from the original tissue, both in *Delphinium* and *Zea*, and in various mosaics produced by Muller (1930*b*) in *Drosophila* by means of X-rays, it was considered probable that the gene does not consist of more than one or two separable parts. In *Delphinium*, Demerec finds that the rate of mutation of rose-α is the same in the cells early and late in ontogeny. This indicates that the time of mutation is limited to a definite period of mitosis which is not interkinesis. If mutation occurred before the division of the gene, at least two cells with the mutated character would always be produced. The fact that one-celled mutations were found at the rate expected, according to the laws of chance, indicates that the mutation occurred at or after the gene had divided into two.

Hertwig (1926) finds in *Antirrhinum* that *globifera* mutates back to normal. It can do so either in the somatic or germ cell tissue, and either in homozygous or heterozygous material. Combination of *globifera* with any of the other allelomorphs normal, *chlorantha*, *nicotianoides*, indicates that certain arrangements increase the rate of mutability of *globifera*. Table 18 illustrates the segregation of various combinations.

TABLE 18

Mutability in Hybrids of the " def.*" Series of Factors in* Antirrhinum majus (*after Hertwig*, 1926)

nic. × $\frac{\text{nic.}}{\text{gli.}}$		nic. 171	$\frac{\text{nic.}}{\text{gli.}}$ 46	normal 124
$\frac{\text{nic.}}{\text{gli.}}$ × $\frac{\text{nic.}}{\text{normal.}}$		nic. 170	$\frac{\text{nic.}}{\text{gli.}}$ 103	normal 422
gli. × $\frac{\text{nic.}}{\text{gli.}}$		gli. 44	$\frac{\text{nic.}}{\text{gli.}}$ 63	normal 24
$\frac{\text{nic.}}{\text{gli.}}$ × F_2	$\frac{\text{nic.}}{\text{gli.}}$ 77	gli. 48	nic. 64	normal 81
nic. × $\frac{\text{chlor.}}{\text{nic.}}$		nic. 169	chlor. 165	

SOMATIC CROSSING-OVER

Stern (1936) has provided strong evidence that some forms of mosaicism, variegation and phenomena attributed to unstable genes are due to crossing-over in the somatic tissue. A group of non-allelomorphic genes, the Minutes, behave as dominants in reducing bristle size, retarding development and roughening the eyes of *D. melanogaster*. Many of these are deficiencies (Schultz, 1929). In their presence, flies, heterozygous for other genes, have a tendency to exhibit a greater number of spots of the recessive phenotypes on the body. Normal flies have 4·6–20% of spots on the abdomen, whereas Minute flies exhibit 8–36·6% spotting. Many and varied experiments were made by Stern to investigate the phenomena. He found that from flies of the constitution $\frac{\text{y yellow}}{\text{sn}_3 \text{ singed}}$, two spots were y, two spots were sn_3 singed, and 11 spots were twin spots where a yellow,

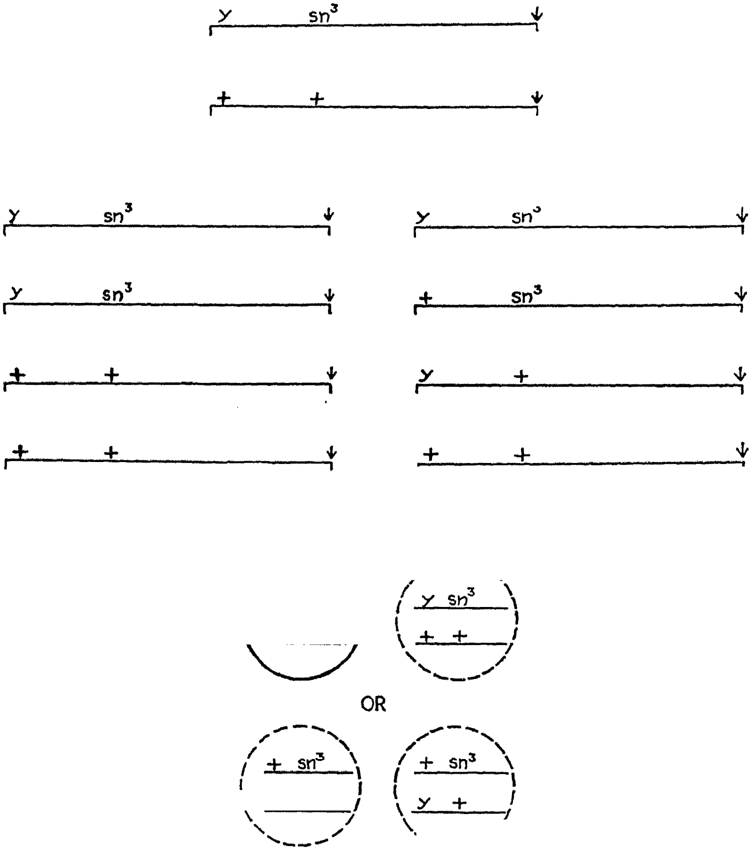

FIG. 23. Somatic crossing-over.

not singed area, and a singed, not yellow area were adjacent to one another. In a larger experiment 124y : 234sn_3 and 147 ysn_3 spots were found in 1,776 individuals. Segregation therefore had occurred in the somatic tissue. When the constitution was $\frac{ysn_3}{+}$ the number of spots was 110 ysn_3, 7 sn_3, 43 y in 1,407 individuals. The production of ysn_3 spots in the first experiment and y and sn_3 in the second simulate the effect of crossing-over. Further evidence confirmed the assumption of somatic crossing-over and indicated some of the conditions. It was found :—

(1) That near the centromere the separation was always equational (contrast meiotic crossing-over).

(2) That crossing-over takes place in the four strand stage and involves two of the four chromatids.

(3) That the frequency of somatic crossing-over is greater near the centromere regions than elsewhere (*X* and III).

(4) That somatic crossing-over occurs in both males and females.

(5) That the position of somatic crossing-over appears to be influenced by the position of the Minute gene. *X*-Chromosome Minutes increase crossing-over in the *X* chromosome especially near the centromere and autosomal Minutes and increase crossing-over in the arm of the chromosome where they are situated.

(6) That the *Y* chromosome may cross over with the *X*.

(7) That the four chromatids taking part in somatic crossing-over are separated in the normal mitotic manner.

The genetical data show that the chromatids at mitosis behave as a unit, and they cannot, therefore, provide evidence for or against the alleged quadripartite structure of the mitotic chromosome.

Evidence for (2) is provided by such facts as y spots from $\frac{ysn_3}{+}$ individuals are not accompanied by sn_3 spots as they would be from two-strand crossing-over—y + and sn_3 +. In four strand crossing-over the result after crossing-over can be (*a*) ysn_3· (*b*) +sn_3 · (*c*) y+ · (*d*) ++· With equational separation (*a*) and (*b*) go to opposite poles to one another and (*c*) and (*d*) go to opposite poles, therefore the two daughter cells contain either (*ac*) and (*bd*) or (*ad*) and (*bc*). Hence the products will be either **ysn$_3$**, **y**+ and **sn$_3$**+, ++ or **ysn$_3$**, ++ and **y** +, **sn$_3$**. Analysis shows that the first of these alternatives in this example gives a separate **y** spot (**ysn$_3$ y**+). **sn$_3$** spots would result from crossing-over nearer the centromere. The fact that no triple adjacent spots of **ysn$_3$**, **y**, and **sn$_3$** occurred indicates that a reduction division has not taken place. Obviously the genetical evidence indicates that if chiasmata are formed by crossing-over they do not remain on the chromosome until metaphase, but each chromosome splits independently of its homologe.

Mosaicism in Maize. The fruit of maize exhibits mosaicism for several characters controlled by genes; **A** and **C** basic genes for colour, **wx** a gene for starchy endosperm, **sh** shrunken endosperm, **Pr** purple aleurone, **su** sugary endosperm and **P** pericarp colour. Emerson (1921–24), Stadler (1930), McClintock (1932), Jones (1935, 1936) have investigated the phenomena and shown that linkage of the genes was reflected in the characters of the spots of different phenotypes. Thus the cross **cwxsh** × **CWxSh** normally gives **CccWxwxwxShshsh** endosperm, completely dominant for colour, starchy, and normal endosperm. **C sh** and **wx** are all on chromosome 9. Emerson (1924*a*) found that out of 127 fruits which showed a change to the recessive character of one of these genes, 121 showed a change to the recessive in the remaining characters. Thus a white aleurone area due to **c** was accompanied by **wx** and **sh** endosperm. On the other hand of 41 mosaic **CSu** fruits, 14 had **Csu** spots and 27 had **Su** accompanied by one or more of **cwx** and **sh**. **Su** and **C** are on different chromosomes and therefore as expected no correlation between **c** and **su** in the mosaic spots is found.

Stadler (1930), continuing this type of experiment, finds that in normal material the frequency of endosperm chimæras varies from 2/1,000 seeds for the chromosome carrying **Su** to 9/1,000 for the chromosome carrying **A**, while the evidence from the **Cwxsh** chromosome indicates that often only a part of the chromosome has fallen out or is deficient. X-raying of **Cwxsh** pollen causes in some cases a greater or smaller part of the chromosome to drop out. It is interesting that mature pollen carrying **A**, when irradiated, sometimes gives rise to deficiency in the endosperm or the zygote independently. This is expected from the fact that one pollen nucleus fertilises the ovum while the other fuses with the fusion nucleus of the embryo-sac. If, however, the pollen is X-rayed earlier, the pollen nucleus has not divided, and it is found that deficiencies in the zygote and endosperm are absolutely correlated.

Stadler also found that the deficient area in endosperms sometimes gave rise to " recovered " cells. Five seeds out of 2,374 resulting from **ARCwxpr** × X-rayed **ARCWxPr** were colourless waxy (**cwx**) except for small spots which were coloured and non-waxy (**CWx**). This recovery of a deficient area also occurred in the plant with regard to the **A** carrying chromosome. " Recovery " is not more frequent per cell in **X**-rayed than in untreated material, but since more deficiencies are produced by X-raying, more recoveries are obtained. The author gives evidence that the recovered areas are not direct cell descendants of normal areas but have resulted from deficient areas. Randolph has shown that deficient areas in the endosperm resulting from X-raying of pollen or of embryos commonly involve the absence of a cytologically detectable chromosome fragment. Stadler puts forward evidence that the X-raying of the pollen either makes the **Cwxsh** fragment of the chromosome drop out or become inactive and recovery is due to the re-establishment of normality. He suggests that the chromosome part becomes inactive and is transmitted without true mitotic division to cell descendants. Recovery, he imagines, will accompany the resumption of full mitotic division by the fragment.

Jones (1935, 1936) suggests that deletions, as found by McClintock (1932), non-disjunction in mitosis, reciprocal translocation, gene mutation and somatic crossing-over (see above) are all involved in the production of mosaic areas in maize fruits. He finds that twin spots involving **C**, **Sh** or **wx** can be formed. For example, in the lightly coloured endosperms of the constitution **Ccc** there are neighbouring spots which are darker in colour and without colour. A " shift " of the **C** gene has taken place to give presumably **CCc** and **ccc** constitutions in these spots. These twin spots indicate that deletion or mutation are not the cause. On the other hand " recovery " (see above), or the appearance of recessive characters in homozygous dominant tissue perhaps cannot be explained by somatic crossing-over alone. Within the twin spot may be found a secondary twin spotting, thus in the darker area of the primary spot **CCc** there may be found a colourless and darker spot as a secondary change. **Wx** may or may not change with **C**, but apparently if one gene is changed at the first change, other genes will be lost, probably at a higher frequency than normal. Paired spots involving **C-Pr**, **Pr-Su**, **Su-Wx** together have been observed after X-rays ; it is believed that reciprocal translocations involving the chromosomes bearing these genes have occurred.

There is a possibility that these data will be largely explained by somatic crossing-over either between non-homologous or homologous chromosomes followed by position effect phenomena.

Position Effect. The Bar locus on the *X*-chromosome of *D. melanogaster* is associated with the number of ommatidia or facets of the compound eye. The size of the facet remains the same but the number of facets varies from about 740 facets in a wild type fly, 325 facets in a Bar-eye fly, to about 26 facets in a double-Bar fly. Mutations from Bar to normal and Bar to double-Bar (ultra-Bar) may take place occasionally (Zeleny (1920), Thompson (1931)). Sturtevant (1925, 1928) made a clever analysis of the phenomena. He showed that any reversion of Bar to double-Bar or to normal eye was accompanied by crossing-over between forked (f) and fused (fu) which lie on either side of the Bar locus. He suggested that the reversion of Bar to double-Bar or to normal eye was due to unequal crossing over at the Bar locus. From an individual $\frac{\mathbf{fB}}{\mathbf{Bfu}}$ unequal crossing-over would produce **fBB**, **fu**, **f** and **BBfu**. Thus both double-Bar **BB** and normal flies O would be produced and accompanied by crossing-over between **f** and **fu.** Individuals of the constitution $\frac{\mathbf{fBB_1fu}}{+}$ (**B**$_1$ is infra-Bar an allelomorph of **B**) were found to give rise to **fB** and **B**$_1$**fu** individuals. As expected, if crossing-over takes place between **B** and **B**$_1$ the products retain the linear order **fBB**$_1$**fu**. Other stocks of the constitution **fB**$_1$**Bfu** gave **fB**$_1$ and **Bfu** progeny. If crossing-over takes place between chromatids derived from one chromosome there should be many more mutations of **B** which are not accompanied by detectable crossing-over. Since these do not occur, we may infer that sister strand crossing-over does not occur.

L. V. Morgan (1931) was able to show that double-Bar and normal could arise as complementary products of one event of crossing-over. A stock carrying two *X*-chromosomes attached together and each carrying B gave rise to a double -Bar female. It is expected that one chromosome would be BB and the other O in constitution in respect of the Bar locus. If so this BB/O female should give rise to about 5% normal-eyed daughters, since 5·1% homozygosis of forked is expected (see p. 100). If, however, the female was BB/B (not expected on the hypothesis) then no normal-eyed progeny is expected. When the female was mated to a normal-eyed male, three out of 53 individuals in the F_1 and 6 out of 102 individuals in the F_2 were normal-eyed. This proportion of normal-eyed progeny is too large to be accounted for by mutation and is that to be expected from homozygosis.

Thompson (1931) also reports two further cases of complementary products, double-Bar and normal from Bar-eyed flies.

The most striking conclusion is therefore that the difference between homozygous Bar and double-Bar is not genic but positional. On separate chromosomes two B genes give the phenotype Bar, but placed side by side on one chromosome, the phenotype is double-Bar. The exact relationship of normal to Bar was formerly a matter of discussion : normal could be a definite wild type gene or an absence. Muller and Prokovieva-Belgovskaya and Kossikov (1936), and Bridges (1936) have, however, shown that normal-eyed individuals have two bands in the salivary gland chromosomes at the Bar locus, while Bar-eyed individuals have four bands—*i.e.*, Bar results from a small duplication. Normal is therefore not a deficiency, and unequal crossing-over probably results from asymmetrical synapsis in the Bar-carrying chromosome.

It should be noted that infra-Bar, super-Bar, baroid, moderate Bar_1 and moderate Bar_2 are other characters associated with the Bar locus. In all cases, except perhaps infra-Bar, the mutations have been accompanied by chromosome inversions or translocation, involving a break at or near the Bar locus. The change in position of the Bar locus in reference to neighbouring genes is believed to be the cause of the reaction effect. Table 19 from Goldschmidt (1928) gives the facet number of various arrangements of Bar, infra-Bar and normal.

TABLE 19

(Adapted from Goldschmidt, 1928)

Eye character.	Formula.	Facet number.
Normal	$+/+$	779·4
Infra-bar	B_1/B_1	320·4
Bar	B_2/B_2	68·1
Double infra-bar	B_1B_1/B_1B_1	38·2
Bar infra-bar	B_1B_2/B_1B_2	26·7
Double bar	B_2B_2/B_2B_2	24·1
Normal bar	$+/B_2$	358·4
Normal infra-bar	$+/B_1$	716·2
Normal double bar	$+/B_2B_2$	45·4
Normal bar infra-bar	$+/B_1B_2$	50·5
Normal double infra-bar	$+/B_1B_1$	200·2
Bar, bar infra-bar	B_2/B_2B_1	37
Infra-bar, double bar	B_2B_1/B_2B_2	24·1

An interesting method of obtaining evidence for position effect is provided by Grüneberg (1937) who found that an inverted *X*-chromosome in *Drosophila melanogaster* with rough eyes became re-inverted. In the animals with re-inverted chromosomes the phenotype of the eye was normal. The breaks for the inversion takes place near rst and in the inert region. Incidentally Grüneberg showed that the inert region between bobbed and the centromere was 10 units instead of 4·5 cross-over units as previously estimated.

Schultz and Dobzhansky (1933) (for Plum$_1$ and Plum$_2$), Stern (1931), Dobzhansky and Dobzhansky (1933) (for Bar) and others (for scute) have shown that some mutations are almost inseparable from chromosome rearrangement or breakage. Losses of material during the breakage or gene mutations as such are equally likely to occur during chromosome rearrangement. Therefore strict analysis is necessary to separate these causes from " position effects."

Mosaic eyes and body characters such as scute have been found to be due to similar phenomena (Muller (1930), Sturtevant and Schultz (1935), etc.). The difficulty of separating possible causes, such as breakage of the gene molecules, gene mutation and positional effect will be obvious. The knowledge that small deficiencies or duplications (insertions) involving no more than one gene may take place, are viable and give different phenotypes without qualitative change of the gene, is of importance in evolution. As Muller (1935) points out a duplication may undergo mutation and provide further variation on which selection can act.

Step Allelomorphism. Serebrovsky (1927), Levit (1930), Dubinin (1929) and Agol (1931), put forward the view that the locus of one gene contains a group of sub-genes, arranged in a linear order and each contributing a definite characteristic to genetic determination. Thus, the following diagram (Fig. 24) pictures the hypothesis in reference to the locus of the multiple allelomorphic series of scute in *D. melanogaster*. The different allelomorphs sc_1, sc_2, sc_3 and sc_4 occupy different regions of the district in the locus, and therefore the author views each of these genes as a sub-gene only partially allelomorphic to another of the same allelomorphic series.

Serebrovsky arranged the characters of bristles controlled by the scute series in a linear order of effect and showed that this order corresponded with that of the supposed position of the sub-genes in the district of the locus. Sturtevant and Schultz (1931) extended this series of characters and showed that each allelomorph had a maximum effectiveness on " definite " bristles, while their effect on other bristles fell off equally on either side. Therefore, each scute allelomorph has a definite effectiveness in inhibiting the development of successive bristles. It is found that sc_4 affects all the bristles, and that sc_1, sc_2 and sc_3 each do so in part, except for the frontal dorsocentral bristle which is influenced by sc_3 and those on the wing influenced by sc_2. If sc_4 were a partial allelomorph of these sub-genes, then in a hybrid between flies with sc_4 and those with other scute factors, only the coinciding characters determined by both sub-genes will appear, and the remaining characters will be of the dominant normal type. Agol found that this was always the case in the scute locus. For example, sc_{10} gives bristles on the head,

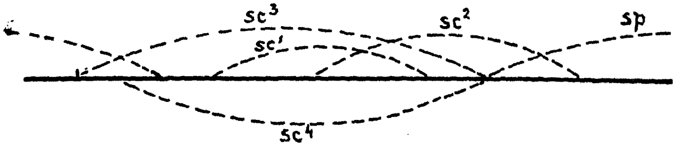

FIG. 24. Diagram of the scute locus in *Drosophila melanogaster* based on the step allelomorphism hypothesis. (Agol, 1931.)

but not on the dorsocentral region, while sc_4 gives the reverse. The hybrid $\frac{sc_4}{sc_{10}}$ gives hairs on both regions. The Serebrovsky school believe that this indicates that sc_4 and sc_{10} occupy two different regions in the scute locus, which together fill almost the whole region of the locus. Where the phenotypic manifestations of two of the allelomorphs are different, reversal to the dominant or normal takes place in that difference only.

Agol points out that $scute_2$ besides affecting the bristles, makes the wings spoonlike and wrinkled. $Scute_4$ does not affect the wings. The neighbouring gene to the right of scute is spoon wing. Therefore Agol suggests that $scute_2$ extends along the chromosome into the district of the locus spoon, but that $scute_4$ does not.

It is said that the scute allelomorphs are only partial allelomorphs. The position and space taken up by one sub-gene allelomorph in the district of a locus may not be the same as that of another allelomorph, but by a step arrangement a long " stair " of allelomorphs is assumed, which passes from one locus to another throughout the length of the chromosome.

A consequence of this theory is that one gene may occupy less space on the chromosome than its allelomorph, and if the genes are an integral part of the composition of the chromosome, one chromosome containing one allelomorph may be shorter than the homologue containing a different allelomorph. This might be detectable by linkage studies. Serebrovsky (1927) and Serebrovsky, Ivanova and Ferry (1929) claim to have detected this difference in length in *Drosophila*.

If allelomorphs are definite physical granules in the chromosome and crossing-over occurs as a result of the breaking of the thin twisted threads at prophase we should expect the substitution of one type of granule for another to have a certain influence on the points and the number of breakages of the chromosomes (Gowens, 1919). On the second chromosome of *D. melanogaster*, black, purple and cinnabar are genes with the loci at 47·5, 53 and 54 units of the genetic map respectively. By careful controlled experiments Serebrovsky (1927) showed that the cross-over value between black and cinnabar was higher when the dominant normal gene was present in the purple locus than it was when the recessive purple was present.

He also found that when the fly was of the constitution **Pr pr**, *i.e.*, heterozygous for purple, the cross-over value for back-cinnabar was less than in flies of the constitution **Pr Pr**. This reduction in the cross-over value he attributes to the perceptible shortening of the chromosome by the dropping out of the gene which is dominant to purple (see Fig. 25). When the fly is heterozygous for purple the two chromosomes will not be symmetrical, and this may interfere with crossing-over. Serebrovsky thus returns to the presence and absence theory, but points out that both it and Morgan's theory may require modification on the view that the gene is divisible.

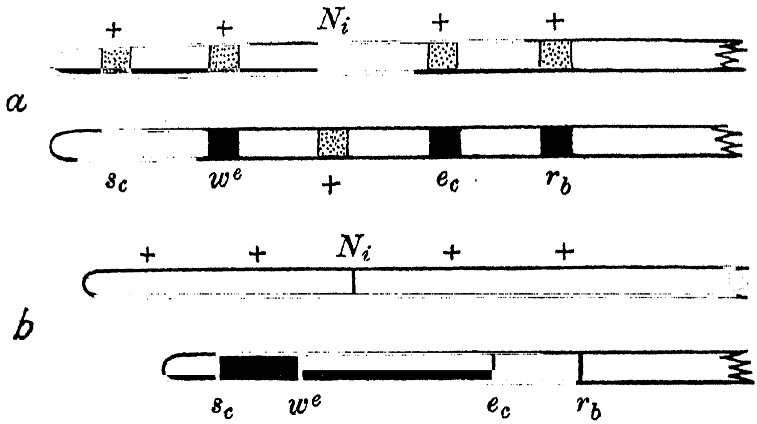

FIG. 25. *a* represents some of the loci of factors in the sex chromosomes of *Drosophila melanogaster*. *b* represents the lengths of the sex chromosomes on the assumption that the recessives and Ni are absences. (Serebrovsky, Ivanova and Ferry, 1929.)

$$\text{Type I} \ \frac{+ \quad + \quad + \quad +}{\text{sc} \quad \text{w}^{\text{e}} \quad \text{e}^{\text{c}} \quad \text{r}^{\text{b}}} \qquad \text{Type III} \ \frac{+\,\text{li} + \quad + \quad +}{\text{sc} \quad \text{w}^{\text{e}} \quad \text{e}^{\text{c}} \quad \text{r}^{\text{b}}}$$

$$\text{Type II} \ \frac{\text{y}+ \quad + \quad + \quad +}{\text{sc} \quad \text{w}^{\text{e}} \quad \text{e}^{\text{c}} \quad \text{r}^{\text{b}}} \qquad \text{Type IV} \ \frac{+ \quad +\text{N}_1 + \quad +}{\text{sc} \quad \text{w}^{\text{e}} \quad \text{e}^{\text{c}} \quad \text{r}^{\text{b}}}.$$

FIG 26.

Later Serebrovsky, Ivanova and Ferry studied crossing-over at the left end of the sex chromosome of *D. melanogaster*. The regions were marked by scute **sc**, eosin $\mathbf{w^e}$, echinus $\mathbf{e^c}$, and ruby eye colour, $\mathbf{r^b}$. The effect of introducing **y**, a recessive situated near scute, **li**, a recessive lethal between yellow and eosin, and **N**$_1$, a homozygous dominant lethal between eosin and echinus, upon the cross-over values between the above genes was examined.

The constitutions of the flies studied were therefore as in Fig. 26.

The authors show that the cross-over values in type I hybrid are lower than II, III or IV, and that type IV showed a marked increase in crossing-over in the region eosin echinus (where **N**$_1$ is situated). **N**$_1$ is probably an absence. Type III showed the greatest increase in the scute-eosin region, while type II showed a general increase.

TABLE 20

Summary of Cross-over Values in three experiments on the X Chromosome of Drosophila melanogaster *involving Flies of four different constitutions* (see Fig. 26, Serebrovsky, Ivanova and Ferry, 1929).

		Regions			Total
		s_c–w^e	w^e–e_c	e_c–r_b	s_c–r_b
Type I	+	0·39±0·05	2·18±0·12	1·32±0·09	3·89
,, II	y	0·61±0·06	2·63±0·13	1·67±0·10	4·91
,, III	l_i	0·59±0·06	2·49±0·12	1·41±0·09	4·49
,, IV	N_i	0·54±0·06	2·83±0·15	1·26±0·10	4·63

		Regions			Total
		s_c–w^e	w^e–e_c	e_c–r_b	s_c–r_b
Type I	+	0·75	4·20	2·55	7·50
,, II	y	0·93	4·02	2·55	7·50
,, III	l_i	0·99	4·16	2·35	7·50
,, IV	N_i	0·88	4·58	2·04	7·50

		Regions			Total
		s_c–w^e	w^e–e_c	e_c–r_b	s_c–r_b
Type I	+	0·59	3·30	2·00	5·89
,, II	y	0·73	3·15	2·00	5·88
,, III	l_i	0·84	3·54	2·00	5·38
,, IV	N_i	0·86	4·49	2·00	7·35

	Regions		
	s_c–w^e	w^e–e_c	e_c–r_b
+	0·39	2·18	1·32
Non- +	0·58	2·65	1·44
Ratio	1·49	1·22	1·09

The authors attribute the increase to the resolution of asymmetry brought about by introducing recessive genes on the chromosome

He also found that when the fly was of the constitution Pr pr, *i.e.*, heterozygous for purple, the cross-over value for back-cinnabar was less than in flies of the constitution Pr Pr. This reduction in the cross-over value he attributes to the perceptible shortening of the chromosome by the dropping out of the gene which is dominant to purple (see Fig. 25). When the fly is heterozygous for purple the two chromosomes will not be symmetrical, and this may interfere with crossing-over. Serebrovsky thus returns to the presence and absence theory, but points out that both it and Morgan's theory may require modification on the view that the gene is divisible.

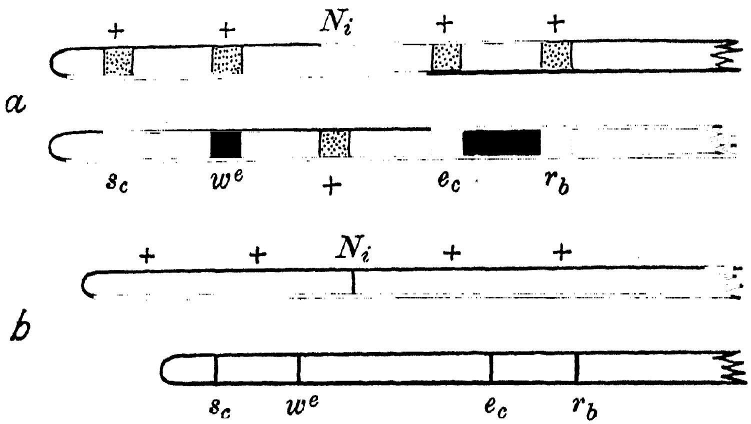

FIG. 25. *a* represents some of the loci of factors in the sex chromosomes of *Drosophila melanogaster*. *b* represents the lengths of the sex chromosomes on the assumption that the recessives and Ni are absences. (Serebrovsky, Ivanova and Ferry, 1929.)

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$$\text{Type II}\ \frac{y{+}\quad +\quad +\quad +}{sc\quad w^e\quad e^c\quad r^b}\qquad \text{Type IV}\ \frac{+\quad +N_1\,+\quad +}{sc\quad w^e\quad e^c\quad r^b}.$$

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	s_c–w^e	w^e–e_c	e_c–r_b
+	0·39	2·18	1·32
Non- +	0·58	2·65	1·44
Ratio	1·49		1·09

The authors attribute the increase to the resolution of asymmetry brought about by introducing recessive genes on the chromosome which carries most dominants. The influence of each recessive gene is most marked in the region of the chromosome to which each belongs, but the influence also extends with less effect to neighbouring regions. The authors assume, then, that the chromosome with the wild type allelomorphs of those they studied will be longer than that containing the recessive genes. Hence a certain asymmetry between the chromosomes results and interferes with crossing-over. When, however, a recessive gene such as y in type II is introduced into the chromosome carrying wild type allelomorphs, the asymmetry is reduced by the relative sizes of y and its dominant allelomorph.

While these experimental facts of Serebrovsky appear to be well substantiated, it is necessary to approach with caution the hypothesis put forward to explain them. Indeed, Sturtevant and Schultz (1931) bring forward evidence that Agol's results could be explained in a different way, more in keeping with the general view. They studied duplications of various portions of the *X* chromosome which included scute itself. Where the duplication includes a considerable portion of the *X* chromosome, as in a translocation to chromosome III of the *X* broken to the right of " white," it is found that scute behaves as a dominant, whereas with smaller portions of the duplicated *X* chromosome it behaves as a recessive. They point out therefore that the expression of scute varies with the balance of the gene to other factors, of which two at different loci on the *X* are known. Hence Agol's results may be explicable by the differential interactions of the different scute allelomorphs with other genes (see also Child, 1935).

Goldschmidt's Physiological Hypothesis. As a result of his work on *Lymantria dispar* and *L. japonica*, Goldschmidt (1922, 1923, 1927, 1931) put forward another theory of factor action which, if true, sheds considerable light on many genetical phenomena. He found that when European and Japanese races of the Gipsy moth were intercrossed, the sex ratio and degree of intersexuality depended on the particular races used, although when inbred each race had a normal sex ratio and behaviour.

The cross, European female × Japanese male, gives normal males but females which are intersexual in the F_1. The intersexual females when crossed with normal males give 50% normal females and 50% intersexual females. The reciprocal cross, Japanese female × European male, gives normal males and females in the F_1, but in the F_2 the males show intersexual tendencies. Different races from Europe and Japan have different degrees of strength of the male and female sex potencies. These were classified and predictions made of the result from any particular cross. If we designate the male potencies as M_1M_2, etc., and the female as F_1F_2, etc., where M_1 is a weak male determiner and M_5 a strong, the various crosses may be symbolised in a factorial manner.

The **M** factors behave as allelomorphs, while the **F** factor is either borne by the W chromosomes (moths have heterochromosomes and are WZ in the female and ZZ in the male) or in the cytoplasm.

A " weak " male $M_2M_2F_3$ × a " strong " female M_3mF_4
gametes M_2 M_3F_4 and mF_4
F_1 $M_4M_3F_4$ M_2mF_4
male × female
$(M > F)$ $(M < F)$
gametes M_2 and M_3 M_2F_4 and mF_4
F_2 $M_2M_2F_4$ M_2mF_4 $M_3M_3F_4$ M_3mF_4
intersexual male female male female
$M = F$ $M < F$ $M > F$ $M < F$

Goldschmidt infers that the particular sex type depends on which sex potency is the stronger during the time of development. The reaction chain of processes originating in the factors, which are supposed to be similar in their action to autocatalysts, are carried on at different but definite rates. The particular reaction process, which is uppermost at the end point of development has the greater influence upon the final character product.

This physiological hypothesis may be applied to almost any genetical result,* but since attention has been previously directed to the Bar and scute cases we will only mention here Goldschmidt's (1927, 1931) interpretation of them. Goldschmidt holds that there is a quantitative difference between normal and the two allelomorphs, Bar and infra-Bar. Their effect on the facet number is similar in kind to the end products of several chemical processes which only differ in the speed of action. The quantity of factor present is proportional to the quantity of the end result with regard to any one allelomorph.

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* Goldschmidt (1938), *J. G.*, draws important conclusions on the evolution of sex determination from the application of the hypothesis to *Streptocarpus*.

As regards the scute allelomorphs Goldschmidt (1931) points out that an interpretation on a physiological basis may be put forward. This supposes that each scute allelomorph sets in motion a train of reaction processes, which in rate of development is a function of the particular factor or factors present. If we have a series of reaction processes, the strength of each proportional to the intensity of the initiating factor, we can arrange these in order of strength up to the point where the character expression is saturated. Thus a step-reaction instead of step allelomorphism summarises Goldschmidt's view.

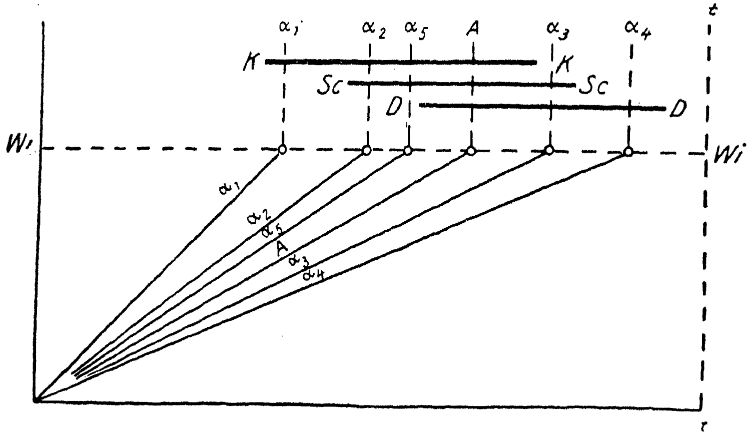

FIG. 27. See text. (Goldschmidt, 1931.)

Qualitative character differences can easily depend on quantitative amounts of factor. Thus some scute factors may only affect the bristles on the head and not those of the scutellum and dorsocentral region of the thorax. The differentiation of the head, scutellum and dorsocentral region may be ended at different periods. Suppose that the different scute allelomorphs produce different rates of development of the reaction processes—then only those parts of the body which are being differentiated at the same time by the reaction processes of other factors will be affected by the scute allelomorph (*cf.* Fig. 27). Where there are two scute allelomorphs, the final character will be determined by the weighted mean of the two reaction processes.

Dominance of one factor over another is thus, according to Goldschmidt, dependent upon the degree reached by the reaction process in the saturation of character expression at the end of the time of development.

The scute example shows that the extent of saturation depends not only on the reaction chain of one factor, but also on its relation to the reaction processes of other factors. In the above figure it will be seen that the head **K**; scutellum **Sc** and dorsocentral **D** region are all affected by the dominant factor **A**, which has saturated the expression of bristles. As regards head bristles, $\mathbf{a}_1$ may be considered dominant to $\mathbf{a}_4$—the head and dorsocentral regions being differentiated at different rates. Therefore the slow rate of reaction of $\mathbf{a}_1$ is able to influence the development of the bristles on the head but not on the thorax. The thorax is supposed to develop quickly and would only be influenced by the factor reaction of the factor $\mathbf{a}_8$. Thus we see in Goldschmidt's theory an assumption of the factor being similar to an autocatalyst in action, and that dominance depends on the saturation of character expression in any particular but defined genetical constitution.

Size of the Gene. Gowen and Gay (1933) have collected and examined the data relating to the number, size and characteristics of genes in *Drosophila melanogaster*. They estimate that with the 175 genes showing visible effects there could be 1,280 recessive and 960 dominant lethals on the *X* chromosome, 9,800 loci of the autosomes would have dominant lethal mutations and 13,100 would have recessive lethal mutations. Altogether, about 14,380 loci are occupied by genes necessary for the life of the organism. The volume of the chromatin occupied by a gene may be estimated from the results of "hits" by X-rays. The volume of a gene locus is calculated as $1\text{–}1{\cdot}1 \times 10^{-18}$ cm^3.

Effects of X-rays. Evidence as to the effects of X-rays upon genes and chromosomes has been accumulating since Muller (1927) directed attention to such radiation for the induction of mutations. Demerec (1937, *bis*), Mather (1934), Mather and Stone (1933), Stone (1933), Fricke and Demerec (1937), Timofeeff-Ressovsky (1934), Huskins and Hunter (1935), have paid particular attention to the phenomena while many others have used X-rays in genetical research. The effect of X-rays is independent of the wavelengths between 0·01 Å and 2·2 Å, and the production of lethal mutations is directly proportional to dosage. Chromosome aberrations such as breaks, deficiencies which in most cases cannot be separated from lethal gene mutations apparently result from direct hits by electrons. Gene mutations which are not lethal are rarer and appear to be of a different nature. Certain loci such as " white " in *D. melanogaster* are more prone to give rise to gene mutations than others.

Huskins and Hunter, Mather and others have shown that X-rays retard and interfere with the normal cell mechanics in a general manner leading to secondary effects of chromosome breakages and subsequent reunions. Several authors have discussed the conditions of breakage and reunion of chromosome parts, but no satisfactory conclusions are yet forthcoming. Demerec has shown that different stocks of *Drosophila* differ significantly in reactions to X-rays, while Catcheside (1936) and others have shown that germinating seeds are more susceptible than resting seeds to X-ray radiation. Both genetical and physiological causes play important *rôles* in controlling sensitivity. It may be that certain stages of the mitotic or meiotic cycle are more susceptible. (See Catcheside 1937, 1938*a,b*.)

Fisher's Theory of Dominance. A theory of dominance, the effect of which resembles the foregoing in some respects, has been put forward by Fisher (1928*a,b*, 1930, 1931).

He pointed out that among 221 mutations in *Drosophila melanogaster* only thirteen were dominant to the wild type, while the remainder were recessive. Of the dominants, all showed incomplete dominance over the wild type. Where there is a series of multiple allelomorphs the wild type is completely dominant over the remainder, but the heterozygotes between any other two show incomplete dominance (see p. 23). If we are to assume that the wild type factor is generally completely dominant over the allelomorphs, as it appears to be, it is evident that the dominance must have been brought about by some particular cause. Fisher sees the cause to be natural selection.

It is known that when first found, a factor mutation is very distinct in type, but after several generations of inbreeding becomes less differentiated from the allelomorph in the wild type. The modification towards a wild type appearance is apparently due to selection of modifying factors which increase viability. Let us suppose that a mutation occurs with a frequency rate of one in a million in a wild population. It is obvious that the heterozygote will be much more frequent in the population than the mutant homozygote. If the heterozygote is 1% less viable than the wild type, the proportion of heterozygotes will be 1 in 5,000, and if it is 50% less viable the ratio of heterozygotes will fall to 1 in 750,000. The mutant homozygotes are proportional to the mutation rate, consequently the number of mutant homozygotes, in comparison with the number of heterozygotes, is negligible.

Selection, therefore, first acts upon the heterozygote. If it were at first intermediate between the wild type and the homozygous mutant, any modification towards the greater viability of the wild type would be favoured by selection. Selection intensity increases rapidly as the viability increases, consequently any heterozygote which was more similar to the wild type in viability would be more rapidly acted upon by selection and might become normal before those with an initially low viability had made any appreciable progress. After the heterozygote is selected to the wild type, selection can start upon the recessive homozygote, which will now be much more frequent in the population. In favourable cases selection may even encourage the recessive to be more indistinguishable from the dominant.

Fisher supposes that selection of the modifying factors changes the character of the heterozygote from that of an intermediate type to that of the wild type. Haldane (1930), however, supposes that mutation of the gene itself may provide sufficient material on which selection would act. Hutchinson and Ghose (1937), Ford (1930) and Fisher (1935) produce evidence in support of Fisher's theory of dominance.

Conclusion. The foregoing theories on genes and gene actions indicate that we have little knowledge of the nature of the gene itself. The presence and absence theory and the step allelomorph theory agree in attributing some quantitative difference to the dominant and recessive allelomorphs. Goldschmidt's physiological theory and Bridges' theory of genic balance (p. 239) agree in assuming that there is a quantitative effect of gene action. In many cases, this quantitative difference in effect between two allelomorphs may be observed, but in all the theories there is assumed to be a qualitative difference between non-allelomorphs and sometimes between allelomorphs. The recent work on structural changes has indicated that characters may be determined by deficiencies, duplications, and relative positions of loci on the chromosome. This at once raises the question whether the gene, as such, exists at all. Goldschmidt (1937, 1938) suggests that the gene as previously understood by geneticists does not exist. The particular arrangement of physico-chemical units on a chromosome in association with other chromosomes and the external environment provide, in his view, for all the known genetical facts. The obvious difficulty of inferring from the character expression the nature of the gene which causes it, necessitates caution in arriving at any conclusion until some quantitative method of measuring genes and their actions can be evolved (see concluding chapter).

CHAPTER IV

VARIEGATION AND CHIMÆRAS

Variegation — Bi-parental Inheritance — Variegation in Ferns — Morphology and Genetics of Chimæras.

VARIEGATION

AMONG plants, variegation is of widespread occurrence. Either the vegetative parts exhibit an irregular mosaic as in *Abutilon Thomsoni* and *Aucuba japonica*, or there is a regular arrangement of stripes or sections of chlorotic tissue between the normal green, or there is a general chlorosis over a larger or smaller portion of the plant.

The mosaic form is often transmitted by a virus from one plant to another. Examples are *Aucuba japonica*, " breaking " in *Tulipa* (Cayley (1928), Hughes (1930)), mosaic in tobacco, potato and other *Solanaceæ* (see " Handb. Pflanzen Anatomie sect. Zelle und Cytoplasma " (1927), and Barton-Wright (1933), for a general account of this phenomenon).

With the above exceptions transmission of variegation from parent to offspring may take place, either by means of nuclear factors or by extra-nuclear means such as the plastids or cytoplasm. Bi-parental inheritance is found in *Antirrhinum*, *Melandrium*, *Pelargonium albomarginata*, Baur (1910), *Hordeum*, Nilsson-Ehle (1913), *Urtica pilulifera*, *Mirabilis Jalapa variegata*, Correns (1909*a*, 1910, 1913, 1915, 1919), *Aquilegia*, *Lunaria biennis*, *Capsicum*, Ikeno (1917), *Barbarea vulgaris*, Dahlgren (1921), Andersson-Kottö (1923), *Zea*, Emerson (1912), Phipps, Demerec *et al.*, among many other plants.

Inheritance through the mother plant only, can take place in *Humulus*, *Primula sinensis*, *Zea*, *Pelargonium vars.*, *Melandrium vars.*, *Mirabilis Jalapa albomaculata*, *Arabis*, *Aubretia*, *etc.*.

THE NATURE OF THE GENES ACTION

The modes of inheritance may be classified as :—

1. Inheritance only through the egg, probably due to plastids or the cytoplasm : *e.g.*, *Primula sinensis*, Gregory (1915) ; *Melandrium album*, Sansome, unpub. ; *Zea*, Emerson (1912) ; Phipps, Demerec, *et al.* ; *Mirabilis jalapa albomaculata*, Correns (1909*a*). But see Imai (1936).

2. Biparental inheritance.

(*a*) Plastid mutation and development under gene control : *e.g.*, *Antirrhinum majus*, Baur (1910), Gairdner and Haldane (1929) ; *Hordeum*, Imai (1928) ; *Urtica peraurea*, *Mirabilis jalapa variegata*, Correns (1920), etc. ; *Pelargonium*, *Zea*, etc.

(*b*) Plastid mutation, autonomous or under gene control : *e.g.*, *Commelina*, *Oryza*, *Chrysanthemum*, *Capsicum*, *Pelargonium*.

(*c*) Plastid mutation without gene control : *e.g.*, *Hydrangea*, *Pelargonium*, Imai (1936)

Maternal Inheritance. In the case of maternal inheritance one may be reasonably sure that plastids instead of nuclear factors act as the carriers of the chlorotic condition. Gregory (1915) suggested that the transmission of diseased plastids through the egg and not through the pollen in *Primula sinensis*, would account for the maternal inheritance of the chlorotic form that he observed. He found diseased plastids in the cells of chlorotic tissue in these plants.

Green, white and variegated green and white plants are found in *Melandrium*. The pollen parent does not influence the variegation of the offspring in the above-mentioned plants and it is found that if the egg arises from sub-epidermal tissue, which is genetically green, the progeny will be green. If it arises from white tissue the progeny will be white, and if it arises from a variegated sub-epidermis the degree of variegation of the progeny depends on the degree exhibited by the particular portion of the sub-epidermis involved.

The cytoplasm and plastids enter the egg from the mother plant but it is of some importance to know whether any cytoplasm and plastids or their primordia enter the egg from the pollen tube.

Correns (1909*a*) made the suggestion that no chloroplasts or cytoplasm of male origin were introduced into the egg and that the transmission of variegation from mother to offspring in *Mirabilis Jalapa albomaculata* was dependent on the cytoplasm or plastids derived from the mother. The question arises as to whether the plastids or some physiological condition of the cytoplasm is the causal agent for white or green plastids. In *Taraxacum, Senecio* and *Mirabilis* the demarcation between normal and chlorotic tissue is well defined. Correns points out that the intermediate zone between two areas is expected to be large when the plastids are mixed in type and are distributed at random to the daughter cells. The cell descendants from an embryonic cell containing a mixture of plastids (white and green) would have a greater chance of containing a mixture than of containing either all white or all green

TABLE 21. *Chlorophyll Deficiencies in Maize* (*Phipps*, 1929)

Character.	Number of factors concerned.
White seedlings, w_1 to w_{11}	11
Dominant white seedlings	1
Xantha seedlings, xn_1, xn_2	2
Pale green seedlings, pg_1 to pg_5	5
Yellow-green seedlings, *yg*	2
Virescent seedlings, v_1 to v_{20}	20
Yellow-white seedlings m_1, m_2	2
Ghost seedlings, *gh*	1
Golden, g_1, g_2	2
White-base leaf, *wl*	1
Argentia, *ar*	1
Fine-striped, f_1, f_2	2
Fine-streaked, *fi*	1
Lineate, *li*	2
Japonica-striped, *j*	1
Green-striped, *gs*	1
Maternally inherited striping	—
Iojap striping	1
Zebra-striped leaves. zb_1, zb_2	2
White sheath	1
Piebald seedlings, pb_1 to pb_4	4
Polka-dot leaves, *pk*	1
Blotch leaf, *bl*	1
	65

For references to the various workers, see Phipps (1929).

plastids. Correns points out that in place of cells showing intergrades of colour, cells are either chlorotic or normal. He therefore assumes that the plasma and not the plastids determines the formation of chlorophyll.

This assumption suggests that the plasma influences the development of the plastids in a similar way to the effect of nuclear factors.

Bi-parental Inheritance. Bi-parental inheritance of variegation may be controlled either by nuclear factors or by the cytoplasm or plastids. Inheritance of variegation governed by nuclear factors is found in *Antirrhinum*, Baur (1910), Chittenden (1927*a*), Gairdner and Haldane (1929), *Urtica peraurea, Mirabilis Jalapa variegata*, Correns (1920, etc.), *Pelargonium chlorina, Zea*, and other species.

Usually green is completely dominant over the non-green form but sometimes, as in *Urtica, Pelargonium, Antirrhinum* and maize, the F_1 plants between green and non-green are variegated. When *Urtica peraurea*, which exists only in the heterozygous state, is selfed, the progeny segregate in the proportion of one white which dies, two peraurea and one green.

The variegated form of *Mirabilis Jalapa* is completely recessive to the normal form and the F_2 segregates in the proportion, three normal and one variegated. The F_2 ratios are not, however, constant. This is probably due to the inconstancy of the variegated form which often sports green branches.

In maize, Emerson (1912), Lindstrom (1918, 1921, 1924, 1925) and Phipps (1929), describe a large number of factors connected with variegation which exhibit peculiar interactions and a variety of expressions.

There are at least sixteen factors, any one of which in the homozygous recessive condition gives virescent seedlings and eleven of which give white seedlings which later may become green.

The various virescent seedlings (Demerec (1924*b*) and Phipps (1929)) may be arranged in a series ranging from white seedlings, which develop a small quantity of chlorophyll at ordinary temperatures, to seedlings which are white at low temperatures only and green at normal temperatures, $\mathbf{v}_5$. *Cf.* Table 21.

The interactions of these factors are of great interest. For example, the three factor pairs $\mathbf{W}_1\mathbf{w}_1$, $\mathbf{W}_2\mathbf{w}_2$ and $\mathbf{W}_3\mathbf{w}_3$, are inherited independently, and the dominants are complementary for normal green colour. On selfing a triple heterozygote, numbers approximating to the ratio 27 green : 37 white seedlings were obtained in the progeny. The factors $\mathbf{W}_5$ and $\mathbf{W}_6$ are linked and both must be homozygous recessive to give a white seedling. $\mathbf{w}_8$ and $\mathbf{w}_9$ are another pair of duplicate factors for white. Demerec (1923).

The authors Lindstrom, Emerson *et al.* have shown that a normal green plant must contain the dominant allelomorphs of all these factors for albinism, together with dominant allelomorphs of a series of virescent factors (**v**). If one of the virescent factors is in the recessive condition another set of factors $\mathbf{L}_1\mathbf{L}_2$ for yellow colour may be observed.

The factor scheme is :—

LVW. **lVW**, green,
LvW, virescent,
lvW, **lVw**, **lvw**, yellow,
LVw, white.

The green plants can therefore be of two types. One, **lVW**, when crossed to a white, will segregate for yellow pigment in the F_2, while the other, **LVW**, will not. Lindstrom (1925) found that the factors $\mathbf{L}_1$ and $\mathbf{L}_2$ react with the factors $\mathbf{W}_1\mathbf{W}_2\mathbf{W}_3$ in different ways. $\mathbf{l}_1\mathbf{W} \times \mathbf{L}_1\mathbf{w}_1$ gives in the F_2 a ratio of 12 : 3 : 1, while $\mathbf{l}_2\mathbf{W} \times \mathbf{L}_2\mathbf{w}$ gives a 9 : 3 : 4 ratio. In the first case the plant of the constitution $\mathbf{l}_1\mathbf{W}$ is green instead of yellow—the factor **W** inhibits the action of the yellowing factor.

Two virescents when crossed together segregate in a 9 : 7 ratio. Only four combinations of the eighteen factors for virescent seedlings were not tested by Phipps.

In addition to the above there are other factors in maize which determine green striping on the leaf—japonica striping **St**, green, yellow and pale yellow stripes **Lj**, and white striped japonica **lj**, as well as the fine striped leaf caused by **ff**.

Plastid Inheritance. Baur's work with *Pelargonium albomarginata* shows that instead of the vegetative parts being irregularly marked with white as in *Mirabilis*, the *Pelargonium* is a periclinal chimæra (see p. 149) of white over green. The epidermis of white and of green tissue are indistinguishable microscopically, but the underlying layers will reflect their genotypical constitution. Baur (1910) and Imai (1936) crossed reciprocally green plants with white over green chimæras, and found that the resulting seedlings were green, white which died and further chimæras.

There is a quantitative difference between the reciprocal crosses.

	Pure Green	Chimæra	White
Green × chimæra .	139	18	4
Chimæra × green .	60	23	0

Thus more chimæras appeared in the progeny of the cross where the chimæra was the female parent. Baur favoured the view that the mode of transmission was not by chromosomes but by plastids in both egg and pollen-tube. Noack (1922), Chittenden (1927*a*) and Baur showed that this green-white chimæra carried the dominant allelomorphs of the *aurea* form of *Pelargonium*. Considerable complication is found in the structure and behaviour of *Pelargonium* (see Literature key for references).

Imai (1936*a,b*) reports further investigations of *Capsicum* variegation (1917*a,b*). Imai finds that the variegated form is recessive to green but does not breed true to type, giving 7 green, 294 variegated and 2 albinos when selfed. He suggests that the gene mutates and the mutated plastids may revert to green. This latter cause gives rise to green ticks in white tissue (also found in *Pelargonium*). Under the influence of the recessive gene, green plastids may mutate to white.

Variegation in Ferns. Andersson-Kottö (1923, 1930, 1931) has made some important discoveries on the inheritance of variegation in ferns.

Sporophytes of *Lastræa atrata* variegated with green and white tissues give rise to green gametophytes from both areas. The succeeding generation of sporophytes are all variegated. Both generations have the same chromosome number and the plants are apogamous. Obviously the development must influence the expression of variegation.

Both the gametophytic and sporophytic generations of *Scolopendrium vulgare* show chlorophyll deficiency. The deficient areas are yellow or pale green in colour. Green gametophytes do not mutate to "pale," but sporophytes even arising from one pale gametophyte (hence homozygous) may mutate in either direction. Sporophytes derived from a green gametophyte are always stable and green.

Genes or plasmatic factors are the means of transmission, and changes take place in the cell-divisions of the sporophyte.

There is a still more complicated behaviour in *Polystichum angulare.* The change from green to white or white to green may occur at any time in the sporophyte. The gametophytes are of four types: (1) green, (2) white dying in the 4–5 celled stage, (3) variegated, always starting with green cells and changing to white which may again give rise to green cells. Although presumably haploid the white and green cells are genotypically distinct. (4) In the early stages these are similar to (3) but later "after-greening" takes place and consequently they cannot be distinguished from normal. To account for these facts Andersson-Kottö suggests that a recessive C factor is in the labile state and able to mutate either to a stable or further unstable state. The reversion may be similar to that found by Stadler and Jones in maize.

These several curious cases require further work to elucidate the manner in which the supposed mutability of the gene and of the plastid under the influence of a gene takes place. It is apparent that the observed variegation has arisen in some peculiar way from one zygote cell, and therefore plastid segregation, gene or plastid mutation must have occurred during ontogeny. (See Imai, 1934, 1936*a*,*b*, 1937.)

Chimæras. Variegated plants which result *de novo* from crosses between two normally green plants or between variegated plants must be constituted by a change in the contents of one or more cells during the early ontogeny of the new embryo. The zygote is supposed to arise from one cell containing female cytoplasm and a nucleus derived from the male and female parents. Nevertheless, the seedling from such a cell is sometimes a well-defined chimæra. Segregation of the white or yellow plastids or cytoplasm from the green cells must have occurred between the stage of the one-celled zygote and that of the many celled chimerical embryo (*cf. Pelargonium,* Baur, Noack, *Silene Otites,* Newton, Sansome (1938), *Œnothera*).

After somatic segregation has taken place the propagation of the ancestral and derivative cells leads to particular and definite results in the morphology of the plant. By artificial creation of chimæras erroneously termed graft hybrids, and by anatomical investigation it has been possible to understand the structure and the genetical and physiological behaviour of plants consisting of tissues of more than one genetical type.

The following artificial chimæras have been formed :—

	Original Species.
Solanum tubigense.	*S. Lycopersicum, S. nigrum.*
proteus.	
Kœlreuterianum.	
Gærtnerianum.	
Darwinianum.	
Solanum, spp.	*S. nigrum, S. sisymbrifolium.*
	S. Lycopersicum, S. melongena.
	,, *S. Dulcamara.*
Cytisus Adami.	*Cytisus purpureus, Laburnum vulgare.*
Cratægo-Mespilus Dardari.	*Cratægus monogyna.*
Asnieresii.	*Mespilus germanica.*
Batesonii.	
Brunii,	
etc.	
Cydonia-Pyrus.	*Cydonia vulgaris, Pyrus communis.*
Peach-almond.	*Amygdalus communis, Amygdalus persica.*

These forms resulted from grafting the original species together. In some cases (*Solanum*) the chimæra arises directly from beneath the callus formed at the graft.

The usual method is to cut back a vigorously growing stock of one species. Into the tissue thus exposed there is inserted a scion of another species. When the two tissues have become attached by growth the scion is cut back. Adventitious shoots arise by the accelerated growth of the procambium on the cut surface. The shoots which arise from the junction of stock and scion will probably contain tissue from both species and will form a chimæra. In the remaining examples of the list, the chimæra has generally arisen at the place of graft after several years of growth and little definitely known as to its mode of origin. It is, however, probable that meristematic activity is induced at the place of graft through the check to the flow of sap which such a change in tissue affords.

The shoot of the higher plant develops from the so-called bud-initials at the apex of the stem. In Monocotyledons such as *Veronica, Hippuris, Ligustrum* and possibly *Cytisus Adami* and *Plectranthas fruticosus*, there are only two layers of bud initial cells, that which gives rise to the epidermis, and that which gives rise to the inner tissue. (Schwarz (1927), Massey (1928)). Hence in these plants one only expects to find chimæras with one layer of one

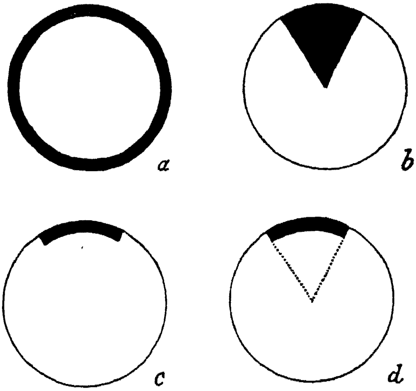

FIG. 28. Cross-sections of stems of different types of chimæras: *a*, periclinal; *b*, sectorial; *c* and *d*, mericlinal. (Jørgensen and Crane, 1927.)

genetical constitution overlying another layer of a different constitution—periclinal chimæras. A sectorial chimæra is constituted when the two different tissues both extend from the centre to the periphery of the stem—a sector or wedge of one tissue inserted in the other. The accompanying diagram (Fig. 28) illustrates transverse sections of periclinal and sectorial chimæras. Such chimæras have been reported in barley, oats, *Chlorophytum* (Collins), *Veronica* and *Ligustrum*. The epidermal tissue of a leaf of a periclinal chimæra will correspond to that of the epidermis of the stem at the place of origin. Thus, if the leaf arises from a genotypically green tissue, the epidermis will be green. The inner layers, at least at the basal part of the leaf, will correspond with the inner layer of the stem. The more distal portions of the leaf are sometimes exceptional and will be discussed later.

The constitution of a leaf of a sectorial chimæra depends upon its position. The leaf may be made up entirely of one tissue or the other, or, if it overlaps, the line of junction of the two tissues, which are arranged side by side in a longitudinal direction, it is made up of the two tissues.

In other dicotyledonous plants, more than two transverse layers of bud initials take part in the laying down of the stem tissues. Therefore it is possible to have three to five genetically different layers in one plant. The outer layer gives rise to the epidermis. The second layer gives rise to the sub-epidermis and the third, fourth and fifth (if present) lay down the endodermis and the stele. The division of labour among the innermost layers differs in different species and perhaps even in one plant (*Pelargonium*, Noack, 1925).

Periclinal chimæras, consisting of one or two layers of one tissue as an envelope over a tissue of different genetic constitution are thus to be expected. *Solanum tubigense* consists of one layer of tomato over a core of *S. nigrum*. *Solanum proteus* has two layers of tomato, while *S. Koelreuterianum*, *Gærtnerianum* and *Darwinianum* have the outer layer or layers of *S. nigrum* and the inner of tomato. *S. Koelreuterianum* has one layer, *S. Gartnerianum* has two layers, and *S. Darwinianum* probably has an outer layer of *S. nigrum*, a sub-epidermis of tomato, and inner layers of *S. nigrum*. Later work of Winkler reported by Lange (1926) indicates that four layers of different genetic constitutions may be formed in one *Solanum* chimæra. *Cratægus-Mespilus Dardari* differs from *Cratægus-Mespilus Asneresii* by having two layers of Medlar over the *Cratægus* tissue in place of one.

It is highly improbable, as Jørgenson and Crane point out, that sectorial chimæras will occur in such forms, if the outer tissue does not completely cover the inner layers. When the inner tissue forms part of the epidermal *anlage* or primordium, the resulting plant will be a *mericlinal* chimæra (see Fig. 28). The difference between the mericlinal and sectorial chimæras consists in the distance to which the outer layer penetrates to the centre of the stem. Mericlinal chimæras are more common than sectorial chimæras.

Lange has shown that three to four different layers of bud initials enter into the formation of the leaf. In the basal parts of the leaf, three to four layers are involved, while at the distal parts there is irregularity in the distribution. This irregularity has been shown to be due to a disturbance of the growth rate of the various layers late in the ontogeny of the leaf. Proliferation of the outer layers is common, resulting in the edges of the leaf being sometimes composed of epidermal tissue only. (Neilson Jones (1934) : see also Weiss (1930) .)

Changes from one type of chimæra to another can occur in one of several ways. For example, a *Solanum* chimæra as it arises from the original formative callus will either be mericlinal or sectorial and rarely, if ever, periclinal in structure. This is due to the fact that the bud initials will consist in one part of one tissue and in another of the alternative tissue. Sectorials will be much rarer than mericlinals, since the former can only arise when there are equal numbers of bud, initials of the two tissues, *i.e.*, when the centre of the bud corresponded with that of the junction of the two tissues.

Although at origin the *Solanum* chimæra is mericlinal it may become periclinal in nature. A simple manner of change from mericlinal to periclinal structure is by the formation of an axillary bud in the region where both tissues are present (one beneath the other). Mericlinals with a different number of layers from that of the original will arise when a bud is formed at the surface junction of the two tissues (at point (*a*) in diagram). These might be classified as regular modes of change. They are expected to occur more frequently in some plants than in others. Therefore a chimæra of *Solanum* is more variable in structure than a chimæra of *Pelargonium* or of a *Liliaceous* plant.

Irregular modes of interchange between periclinal, mericlinal and sectorial chimæras arise through the bud initials, which normally give rise to one part of the plant (sub-epidermis, stele, etc.) suddenly entering into the formation of a different tissue. Such irregularities probably arise through injury, or some other disturbance of relative rates of propagation of the several layers. Thus a periclinal chimæra with one layer of *S. nigrum* over *S. Lycopersicum* may give rise to a shoot of pure *S. Lycopersicum* by a bud whose epidermis is formed from *Lycopersicum* in place of the *nigrum* tissue. Doubling of the outer layers to form two layers of *S. nigrum* in place of one is also known to occur.

In *Cytisus Adami*, *Cratægo-Mespilus*, *Pelargonium* and other chimæras, the inner or outer component tissues alone may produce a branch or leaf or flower. Hence in certain parts of the chimæra the original tissues, whether of stock, of scion, or of normal or mutant origin may be recovered. Buder injured the bud of *Cytisus Adami*; the outer tissue of *Cytisus* was injured, and the inner Laburnum component gave rise to a pure Laburnum shoot.

The above interpretation of chimærical structure was first suggested by Baur (1909). It is founded on well-established facts of plant ontogeny. Noack (1922) and Collins (1922), however, have suggested that somatic segregation into white and green tissues by one or more apical cells would give rise to a variegated plant. Noack supposes that there is a labile state in the apical cells of a variegated chimæra. During the transition from the meristematic to half meristematic condition, the cell undergoes a "Determination process" to white or green. For example, a sub-epidermal cell might lay down green tissue by tangential divisions and white tissue by radial divisions, giving rise to a periclinal chimæra of white over green. Collins analysed *Chlorophytum elatum* and *Comosum* vars. *mediovariegata* and *albomarginata*. The *albomarginata* is a one-layered white over green periclinal chimæra while *mediovariegata* is green over white. Collins supposes that there is an orderly segregation of an inhibitor for chlorophyll production in the somatic meristems and that the dermatogen occasionally may form internal tissue, by transverse divisions, as well as the epidermis by more normal tangential divisions. (Compare also Andersson-Kottö, 1931.)

Among the consequences of the theories of Noack and Collins are (*cf.* Chittenden, 1927):—

1. There is only one true periclinal chimæra—that with one layer of tissue over layers of different genetical constitution—monochlamydious.

2. Polychlamydious periclinal chimæras, *i.e.*, those with more than two layers of different genetical constitution should not occur.

3. Sectorial chimæras may occur by this method, but the leaves will bear no relationship in chimærical structure to the part of the stem from which they arose.

While the discovery of polychlamydious periclinal chimæras in *Solanum* by Winkler and the knowledge that predictions can be made from the character of the stem as to the character of its leaves are serious obstacles to Noack's view, it should be remembered that Andersson-Kottö's experiments in ferns (see p. 146) suggest that a meristematic cell may change its state during development. There is also evidence from the anatomical work of Noack and Lange (1927) that some varieties of *Pelargonium* do have irregular proliferation of cells in the ontogeny of the leaf.

Morphology of Chimæras. The outward appearance of chimæras can be interpreted in terms of internal structure as the result of work by Jørgensen (1928), Winkler (1909, 1916, 1925), Daniels (1904–1930) and Sansome (1930). The characteristic white or green areas of the leaf of *Pelargonium, Buxus, Melandrium,* etc., depend on the inner tissue—the epidermal tissue has generally colourless plastids. The gross shape of the leaf depends on the inner tissue. In *Solanum, Cratægus-Mespilus* and *Cytisus Adami* it is found that if the sub-epidermal and inner layers consist of layers which normally produce either compound or dissected leaves, the chimæra will have compound leaves. Appendages such as hairs, or glands and scent usually depend on the epidermal tissue. For example, it is found that chimæras of *Solanum luteum* over tomato have not the epidermal hairs or scent of tomato. The chimæra of tomato over luteum, however, possesses these characteristics. It is interesting in this connection to note that when a chimæra is formed of one layer of *S. nigrum* on *S. sisymbrifolium* the characteristic spines of *sisymbrifolium* which are of sub-epidermal origin are developed to a slight extent.

The details of shape and minor characters of the leaf correspond to those of the species which constitutes the outer layers, in a chimæra which has the epidermis and sub-epidermis constituted from one species. Generally, however, the leaf is distorted in the centre, if the inner tissue is composed of a compound-leaved species such as *S. Lycopersicum.* If there are two layers of the simple-leaved *S. luteum, nigrum* or *guinense* over *S. Lycopersicum* the leaf is often asymmetrical and twisted. This is probably due to the genetic differences controlling rates of development of the inner and outer layers.

The flowers and fruits often show the effect of chimærical structure. The artificially produced chimæras of *Solanum, Cytisus Adami* and the *Cratægus-Mespilus* " graft hybrids " are prominent examples which exhibit the chimærical nature of the flowers and fruit. For example, *Cytisus Adami* has three types of flowers (1) those of *Cytisus purpureus,* (2) those of *Laburnum vulgare,* and (3) a type intermediate between the two species. The last type is purplish in colour and sterile.

The flowers of *S. Koelreuterianum* and *S. Gærtnerianum* are white but generally show a yellow stripe in the centre. The flowers of *S. nigrum-sisymbrifolium*–1 (one layer of *s.* over *n.*) are far from being intermediate between the two species. The petals are generally cut to the base like *nigrum* and have the shape of *sisymbrifolium.* Therefore the flowers of the chimæra may grow to a large size. At first they are white but later show the characteristic blue colour of *sisymbrifolium.* The chimæra of *S. Lycopersicum-luteum*–1 never bears flowers. A cork layer is found in the place where the flower is expected.

The apparent dissimilarity of the morphological features of the chimæra from those of the original species led some workers to the view that the so-called graft hybrid was similar to a seed hybrid—it was supposed that actual fusion had taken place in the formation of the graft hybrid. This point of view is reviewed by Weiss (1930) and need not be more than referred to here since proof of the nuclear fusion (and subsequent reduction division) has not yet been provided. The facts upon which this viewpoint is based can be explained satisfactorily by the ontogenetic interpretation outlined above. For example, it has been found that certain anatomical features (*e.g.,* shape of epidermal cells in *Cratægo-Mespilus,* Haberlandt (1926, 1927, 1930), Weiss (1930), number and shape of flower parts, and leaf shape) were either intermediate or different from those of the original forms (*cf.* Weiss, 1930).

Physiological interactions between the genetic properties of the component tissues will result in considerable morphological modification and physiological changes of the chimæra when considered as a whole. It is known that in the artificial chimæras of *Solanum* the development of pigment in the flower or of chlorophyll in the leaf is dependent upon the genetic properties of the tissue underlying the cells of manufacture as well as upon the characteristics of these cells. In *Pelargonium zonale,* "Happy Thought," having green edges to a yellow leaf, which is probably a periclinal chimæra of two layers of green cells over a yellow core, the outer parts of the leaf are green and the centre of the leaf is yellow. No green tissue can be detected overlying the yellow in the centre of the leaf. It was found, however, that if the green tissue is close to yellow tissue in "Mrs. Pollock" it is bleached and contains no chlorophyll. It is therefore probable that the centre of the leaves of "Happy Thought" are yellow through the bleaching effect of the yellow core upon the overlying green tissues (Chittenden, 1928). At the edges, there will be little or no yellow tissue at all. The fact that the distal edges of the leaf of many plants (spp. of *Pelargonium, Veronica, Hydrangea, Spiræa,* etc.) may have a character distinct from the centre of the leaf is puzzling and has misled some workers. It should be remembered that at the centre of the leaf the tissues are derived from the same sources as the comparable tissues of the stem. At the periphery of the leaf the sub-epidermis and inner tissues are generally absent; the edges of the leaf are generally formed by tangential divisions of the epidermal layer. Naturally, the change-over from sub-epidermal to epidermal development of the leaf edge is not regular and anomalies such as islands of cells of sub-epidermal origin will sometimes be found at the edge of the leaf among those of epidermal origin. Chittenden (1927) describes several peculiar chimæras (*Pelargonium* "Freak of Nature," *P. zonale* Variety "A," *Spiræa variegata, P.* Golden Brilliantissima, *Hydrangea hortensis nivalis* and *H. hortensis variegata*) which may all be found to be of this nature.

These and other peculiarities of chimæras indicate that their behaviour is not so simple as the rough outline of the ontogeny would suggest. It appears that the interactions between genetically dissimilar tissues do induce changes in the morphological and physiological characteristics of those tissues. The mutability of the plastids must also be considered as a possible source of variation.

One of the most interesting consequences of the chimærical structure is that of differential reaction to fungal infection. Klebahn (1918) discovered that the reactions of the Solanum artificial chimæras to *Septoria lycopersici* which attacks tomato but has little effect on *S. nigrum*, were different. The following table illustrates the resistance to the fungal attacks :—

	Infection.	Epidermal layers.
S. proteus	Heavy	Two layers of tomato.
S. tubigense. . . .	Slight	One layer of tomato.
S. Gærtnerianum . . .	Slight	Two layers of *nigrum*.
S. Kœlreuterianum . .	Heavy	One layer of *S. nigrum*.
S. Lycopersicum . . .	Heavy	Tomato.
S. nigrum	None to sli	*S. nigrum*.

It will therefore be seen that the presence of tomato or *S. nigrum* tissue in the epidermis and sub-epidermis determines the amount of infection by *Septoria lycopersici* which develops the fructifications in the sub-epidermis.

Fischer (1912) inoculated *Cratægo-Mespilus Asnieresii* and *C-M. Dardari* with *Gymnosporangium clavariæforme*, which affects the hawthorn but does not attack the medlar. In the first case the chimæra was slightly affected, while in the case of *C-M. Dardari* no infection was possible. *C-M. Asnieresii*, it will be remembered, is supposed to consist of two layers of *Cratægus* over *Mespilus*, while *C-M. Dardari* has only one layer of *Cratægus*. Other cases are given by Bond (1936).

It is a well-known fact that a chimæra does not propagate itself from seed. It either gives rise to seedlings of one or more of the pure component tissues or it is sterile.

The sub-epidermis generally gives rise to the egg and pollen, and the constitution of that tissue therefore controls the characteristics of the resulting seed. Examples of this phenomenon are to be found in *Pelargonium*, *Myosotis*, *Solanum*, etc. (*cf.* Chittenden (1926, 1927), Bateson (1916–1925)).

The adventitious stem cuttings from the roots of chimæras are of endogenous origin. Therefore by taking cuttings it is possible to analyse the inner tissues of a periclinal chimæra. Escot, a regal *Pelargonium*, has white-coloured grounds to the petals. The root cutting of Escot has pink-coloured petals. Seed from both Escot and the root cutting of Escot gives rise to white and to pink-flowered plants. This result is easily explained on the assumption that the tissue of Escot root cutting is heterozygous, pink being dominant to white flower colour. Escot gives rise to both pink and white progeny although it has the recessive white petals. This is due to the fact that the sub-epidermis is of the constitution of the Escot root cutting.

There are several peculiar cases where either the chimæra is sterile or it does not give rise to seed of sub-epidermal origin. Sterility may be due to (1) prevention of fertilisation through interference with the normal processes of pollen tube growth by a stigma of different genetical constitution, or (2) the production of gametes of abnormal type.

A striking example of the influence of tissues of dissimilar constitution upon fertility of a chimæra is seen in the artificial chimæra *Solanum nigrum-sisymbrifolium*-1 which gives haploid *S. nigrum* plants from seed. It has been known for some time that when *S. nigrum* is pollinated by pollen from some other species of *Solanum* no fertilisation takes place, but that the stimulation of the pollination induces the development of the unfertilised egg. In the chimæra we may suppose that the pollen arising from the tissue of *S. nigrum* is unable to penetrate the style which is chimærical in nature. The stimulation resulting from the pollination, however, induces the egg (of *S. nigrum*) tissue to develop without fertilisation. *Hydrangea nivalis* and *Pelargonium* Freak of Nature have sterile flowers although the component tissues are fertile either as plants of one tissue or in different chimærical arrangements. (Chittenden, 1925.) It is probable that these cases are similar to that of *S. nigrum-sisymbrifolium* although there is the possibility that abnormalities in embryo sac and pollen formation can be caused by the presence of two dissimilar tissues. Examples of the effect of the latter phenomena are probably to be seen in the female sterility of *Cytisus Adami* and *Pelargonium* Salmon Fringed.

Those chimæras which form the mesophyll of the leaf edges from the epidermis and not from the sub-epidermis are either sterile or give seed of epidermal origin (*Hydrangea* hort. *nivalis* ; Chittenden (1925)) or give seed of both epidermal and sub-epidermal origin (*Hydrangea* hort, *variegata* ; Chittenden (1925)). On the established view that the carpel is of foliar nature it is to be expected that changes in the constitution of the leaf tissues will be reflected in the constitution of the ovule. *Hydrangea variegata* (green over white periclinal) is of particular interest, since Chittenden points out that seed taken from the branches whose leaves have numerous and larger green lobes gives rise to more green plants than seed from branches whose leaves have fewer green lobes and more white edges.

Mericlinal, periclinal and sectorial chimæras occur in the frequency expected from anatomical investigations. For example, sectorials are more common than mericlinals in Monocotyledons and Dicotyledons with only two layers of bud initials, while mericlinals are frequent and sectorials are very rare in those Dicotyledons with more than two layers of bud initials. Modes of branching, leaf formation and flower development are reflected in the behaviour of the regular chimæras.

There are, however, a number of chimæras which constitute a class by themselves. These irregular chimæras, if they can be called chimæras, raise problems not met with in the regular chimæra. Mosaics of colour, flaking of leaves, and petals are distributed as larger or smaller patches or flakes of colour in a ground of different type. The distribution as in *Dahlia variabilis* "Union Jack," may simulate a regular chimæra, but generally the flaking is irregular and cannot be classified by anatomical methods. Generally the cells in a mosaic plant differ regarding their content of anthocyanin pigment (*Antirrhinum, Dahlia, Delphinium, Primula, Lathyrus*), but occasionally the pigment is a flavone (*Antirrhinum, Dahlia*).

A peculiarity of mosaic forms is that somatic segregation takes place at definite time in the life cycle in a particular part of the plant. In different plants and in different branches of one plant variation in the time of segregation, however, is frequent. Consequently, mosaics consisting of numerous isolated cells of mutant type are found when the segregation takes place late in the ontogeny of the leaf or petals. Large patches of one colour are found when the segregation occurs at a slightly earlier stage (see p. 120).

It is curious that in most species a flower either has a fine mosaic of many isolated cells of mutant type or has a coarse mosaic of fewer but larger groups of cells of one type, and generally does not have a mixture of the two (coarse and fine mosaics).

It would appear that the onset of the expression of the segregation process is controlled by definite time factors of the same nature as those known to control genetic factor action.

As might be expected from the irregularity in the distribution of the dissimilar cells in one plant, sports to self-colour or to white or to a finer or coarser mosaic form are frequent in these irregular "chimæras." Fine mosaics give rise more frequently to branches with flowers having apparently only the ground colour of the mosaic. Coarse mosaics are more unstable than fine mosaics and more frequently give rise to self-coloured forms (see p. 121).

These phenotypic changes are generally but not always accompanied by genetical change. In general the frequency in which the self-coloured white and mosaics of different grades occur in the progeny depends upon the types of mosaic exhibited by the parent. The mean and mode of the frequency of the type corresponds with the grade of the parent.

Reference should be made to Chapter III for further examples of mosaics, and to Chittenden (1925), Imai (1936), and Krenke (1933) for a fuller discussion of the subject.

It is imperative that more work be done upon mosaic forms in order to discover their relationship, if any, to regular chimæras and to somatic crossing-over. Some peculiar cases of breeding behaviour may also be similar to these mosaic forms. Until the mosaic itself is understood, it is not profitable to utilise this explanation for such phenomena as that of Andersson-Kottö's variegated ferns (see p. 146).

CHAPTER V

THE ORIGIN OF POLYPLOIDY

Introduction — Somatic Doubling — Doubling during gametogenesis.

Introduction. Each type of chromosome present in the basic or haploid complement of an organism is represented twice in the diploid form. If the haploid set be represented by *n* then the diploid number of chromosomes will be 2*n*, the triploid 3*n*, tetraploid 4*n*, and so on. The realisation that polyploid forms are extremely common in nature, has considerably changed the viewpoint of geneticists. The first reported case of tetraploidy under controlled conditions was that of the *gigas* mutant of *Œnothera Lamarckiana* which appeared in the cultures of de Vries. This plant was shown by Gates (1909) to have larger cells and larger nuclei containing 28 chromosomes in place of the usual 14 of the diploid (Lutz, 1907). Since then numerous polyploids have arisen in experimental material. Among the best known are: *Primula Kewensis* (Newton and Pellew, 1929), *Raphanus-Brassica* (Karpechenko, 1924, 1927*a*,*b*, 1928), *Solanum nigrum*, *Solanum Lycopersicum* (Winkler (1916), Jørgensen and Crane (1927) and Jørgensen (1928)), *Primula sinensis* (Gregory (1914), Gregory, de Winton and Bateson (1923)), *Nicotiana sp.* (Clausen and Goodspeed (1925), Rybin (1927) and Brieger (1928*a*)), *Crepis* (Navashin, 1925*b*), *Phleum* (Gregor and Sansome, 1930), *Musci* (Marchals (1907) and Wettstein (1924*a*)), *Datura Stramonium* (Blakeslee, Belling and Farnham, 1923).

In a diploid, the chromosome number of the gametophyte is haploid and generally corresponds with the basic number, except in certain cases generally known as diploids, which later will be shown to be complex or " secondary polyploids " and not true diploids in the accepted sense of the word (see p. 222). In polyploids, however, the chromosome number of the gametophyte does not correspond to the basic number. For convenience 2*n* is used to represent the somatic number and *n* the haploid or gametic number of a particular plant, while x represents the basic number of the group to which the plant belongs.

The lists of Tischler (1927, 1931, 1936) and Gaiser (1926, 1930*a,b*, 1933) give the chromosome numbers of several thousand flowering plants. These plants belong to about five hundred genera of diverse natural orders. About one-sixth of the genera included, consist of species which have straight polyploid numbers, *i.e.*, they are multiples of a common basic number x. For example, the species of *Chrysanthemum* have somatic numbers 18, 36, 54*, 72*, 90*, *i.e.*, $x = 9$ (Tahara, 1921). *Solanum* species have somatic numbers 24, 36, 48, 60, 72, 96, *c.a.* 100, 108, *c.a.* 144 therefore $x = 12$ (Jørgensen (1928), Jørgensen and Crane (1927), Vilmorin and Simonet (1927*a,b*, 1928)). In the first case the species with the highest chromosome number has ten sets of the basic number of the genus (decaploid). Other genera such as *Solanum* may have species with an even higher multiple number (*cf.* Wanscher (1934), Fernandes (1931)).

In a few cases the species of a genus may be divided into two distinct polyploid series. *Papaver* has species with chromosome numbers 14, 28, 42, 70, and 22, 44 (Ljungdahl, 1922, 1924), and the two basic numbers are $x = 7$ and $x = 11$. We shall see later that this diversity in the basic number is significant in defining inter-relationships. Winkler introduced the word *heteroploid* to include both the straight polyploids and those plants which have irregular numbers such as $2x + 1$, $3x - 1$, etc. Täckholm (1922) further divided heteroploid numbers into *euploid, i.e.*, straight polyploid and *aneuploid*, *i.e*, irregular numbers.

It has been found that polyploids may originate in either of two ways.

(1) By doubling of the chromosome number in the somatic tissue.

(2) By formation of gametes containing either the unreduced number of chromosomes or at least containing more than the haploid complement of chromosomes.

The genetical consequences of these two methods of doubling of the chromosome number may be different for the following reasons. Where the doubling takes place in the somatic tissue, the resultant polyploid form naturally contains a double complement of the chromosomes and factors present in the original form. Hence there is no qualitative difference, but a quantitative difference in factor content between the diploid and its derivative tetraploid forms. On the other hand, formation of gametes with more than the haploid complement of chromosomes may or may not give a similar result to that of somatic doubling. If a gamete is formed by a division, in which the reduction phase, characteristic of meiosis, is nullified, and if this gamete is fertilised by one similarly formed in the same plant, then the resulting polyploid will have a chromosome constitution identical with that of a polyploid formed by somatic doubling. If on the other hand, polyploid gametes are formed in any other way the chromosome complement resulting from their union will be different from the complements arising from somatic doubling.

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* The haploid numbers were counted.

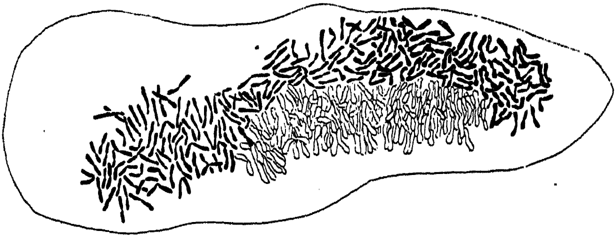


FIG. 29. Cell of *Allium Cepa* resulting from previous treatment with colchicine. Normal mitosis involving ±500 chromosomes has restarted. (Levan, 1938.)

Somatic Doubling. Evidence of the method of origin of particular polyploids is difficult to obtain among wild forms. Various methods for increasing the frequency of cells with a doubled number of chromosomes are now available. Randolph (1932) uses heat on the inflorescences of *Zea* at the time the zygote is beginning to divide. This method has been found useful in maize, rye, barley and wheat (Muntzing, 1937). Tetraploid branches ($2n = 48$) were produced on diploid *Datura* plants ($2n = 24$), chiefly after cold treatment, and gave fertile tetraploid progeny (Blakeslee and Belling (1924*a,b*), Blakeslee and Avery (1937)). Treatment with chemicals such as chloral hydrate, quinine sulphate (Nemec, 1904, 1910) produced irregularities in cell division from which cells with new chromosome numbers could originate.

Colchicine, however, has been found to be the most effective chemical to induce the formation of polyploids. Blakeslee, Avery, Nebel, Ruttle, Eigsti and Jones showed that water-immersion of seeds, sprays or lanolin pastes containing up to 0·4% of colchicine inhibited the separation of chromosomes at metaphase (Blakeslee and Avery (1927), Nebel and Avery (1938), Denham (1938), Levan (1938)). Levan studied the behaviour of colchicine treated root-tips of *Allium*. The centromeres do not separate and no spindle is formed ; the chromosomes therefore lie in pairs scattered in the nucleus. After some delay these are included in one cell to give rise to a cell with the double number of chromosomes. Several aberrant divisions may however take place giving rise to an increasing number of chromosomes in the daughter-cells. Obviously the relative rates of growth of cells with different chromosome numbers considerably control the production of shoots with those numbers. The method is one of considerable importance and should give valuable help in the future.

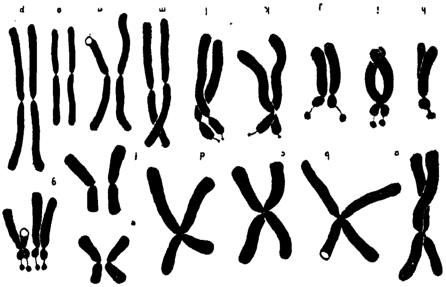


FIG. 30. The division of the centromeres within the pairs of chromosomes treated with colchicine. *Allium Cepa a-b, k-l; A. fistulosum i-j, m-p.* (Levan, 1938.)

Parts of the sporophyte (seta or sporogonium) of mosses can be regenerated on agar (Wettstein, 1924*a*) to produce a protonema (gametophytic generation) thus eliminating the normal reduction division ; therefore, a gametophyte with the diploid number of chromosomes is produced. This gives rise to a sporophyte with a tetraploid number. The process can be repeated to produce an octoploid, but in mosses as in other forms it is found that the vitality of forms with higher chromosome numbers is low.

Polyploid forms of *Solanum* have been obtained as adventitious shoots from diploid plants. Jørgenson and Crane (1927), Jørgenson (1928) and Sansome (1930) developed Winkler's method (1916) and found that decapitation of a rapidly growing young plant induced rapid regeneration on the cut surface. About 6% of the adventitious shoots thus formed had double the number of chromosomes of the original plant. Schavinskaya and Karpechencko report several instances of doubling of the chromosomes in the somatic tissue of *Brassica* species and hybrids with *Raphanus* and mustard. An octoploid cabbage has been obtained by this method. (See *Bull. Appl. Bot. U.S.S.R. 7*).

Jørgenson (1928) suggested that tetraploid cells take their origin from the formation of binucleate cells by a nuclear division without the concomitant cell wall formation. This endo-duplication process has been histologically studied by Mather (Sansome, 1933) and by Lindstrom and Koos (1931) who show the presence of binucleate cells in the regions from which shoots with the doubled number of chromosomes would be formed. Changes in chromosome number are not of rare occurrence in the somatic tissue. Some examples of the occurrence of polyploid cells are referred to in Table 22.

TABLE 22

Occurrence of Polyploid Cells in Plants

Crepis	$2n$	$4n$	Navashin (1926)
,,	n	$2n$	Hollingshead (1930)
Datura	n	$2n$	Blakeslee and Avery (1937).
,,	$2n$	$4n$	Satina, Blakeslee and Avery (1937).
Kniphofia	$2n$	$8n$	Moffett (1932).
Lycopersicum	$2n$	$4n$ & $4n+4$	M. Lesley (1925).
Narcissus	$2n$	$2n+1$	Philp (unpub.).
Nicotiana	$2n$	$4n$	Webber (1930).
,,	n	$2n$	Ruttle (1928).
Pisum sativum	$2n$	$2n+1$	Strasburger (1907).
Primula sinensis	$2n$	$4n$	Philp (unpub.).
Rubus	$3n$	$6n$	Crane and Darlington (1927).
Scilla	$2n$	$2n+1$ $2n-1$	Darlington (1926).
Sorghum	$2n$	$4n$	Huskins and Smith (1932).
Spinacia	$2n$	$4n$	Stomps (1910), de Litardiere (1923).
Tragopogon pratensis	$2n$	$4n$	Winge (1917).

DOUBLING OF CHROMOSOMES IN THE SOMATIC TISSUE

Aquilegia chrysantha × *A. nana,* Skalinska (1935).
Brassica Napus × *B. campestris.* Frandsen and Winge (1932).
Datura species. See Blakeslee and Avery (1937).
Lycopersicum esculentum. Jørgenson and Crane (1927), Sansome (1930, 1933), Lindstrom and Koos (1931), Lesley and Lesley (1930).
Nicotiana. Clausen and Goodspeed (1925).
Primula Kewensis. Newton and Pellew (1929).
Solanum species. Jørgenson (1928), Winkler (1916).
Vicia macrocarpa × *V. sativa.* Sveschnikova (1929).
Zea Mays. Randolph (1932).
Nicotiana glauca × *Tabacum.* Sarana (1935).

It has been found that a considerable proportion of the twin seedlings of Gramineæ have one member of the twin with 50% more chromosomes, *i.e.*, a diploid parent will give a triploid (Müntzing, 1937). Haploids have been found among the twin seedlings of cotton, flax and *Datura* (Satina, Blakeslee and Avery (1937), Harland (1936), Kappert (1933)).

It is worth noting that some species such as *Datura, Viola* and *Nicotiana* show considerable chromosome changes, whereas other species, such as *Antirrhinum,* do not appear to have such striking chromosomal variations.

The origin of the tetraploid *Primula Kewensis* is a good example of the doubling of the chromosome number in the somatic tissue. It was first reported by Digby (1912) and later by Newton and Pellew (1929). The sterile diploid hybrid between *P. floribunda* ($2n = 18$) × *P. verticillata* ($2n = 18$) produced one branch with fertile flowers. Tetraploid offspring ($2n = 36$) which bred approximately true were obtained from this branch, which had double the chromosome number of the rest of the plant tissue.

Nicotiana glutinosa ($2n = 24$) × *N. Tabacum* var. *purpurea* ($2n = 48$) normally gives sterile triploid hybrids. Clausen and Goodspeed (1925), however, found one F_1 plant which set seed when selfed artificially, but not when naturally pollinated. The selfed progeny were found to be hexaploids ($2n = 72$), and were also reasonably self-fertile and cross fertile with the parent species. These workers believed that this particular F_1 plant had doubled its number of chromosomes soon after fertilisation and therefore had become a hexaploid. This hexaploid is known as *N. digluta*.

Doubling in gametogenesis. Polyploids more frequently originate by irregularities of meiosis in the parents than from doubling of the chromosomes in the somatic tissue. Cytological evidence as to the methods of origin of polyploid gametes is abundant (see Darlington, 1930*a*, 1937). These may be grouped under three heads :—

(*a*) Nullification of the first or second division of meiosis.

(*b*) The formation of binuclear germ-mother cells—syndiploidy.

(*c*) The first division of meiosis is completely suppressed.

It is not within the province of this book to analyse the many known cases where irregularities of gametogenesis have occurred. Darlington (1937, Chapter VI and Chapter X), deals fully with the data. The facts, however, may be summarised in so far as they bear on genetical problems.

The first type of abnormality—nullification of the first or second division of meiosis—arises generally through the presence of one or more chromosomes on the equator of the metaphase spindle between the two anaphase groups. The separation of these groups is thus prevented. Lagging of chromosomes on the spindle at the first division may arise from reduced bivalent formation at prophase, or from irregular association of chromosomes caused by inversions or other structural changes. Lack of metaphase pairing can be due to genetical causes, low chiasma frequency, lack of homology or to structural causes. Lagging of chromosomes at the second division may result from a previous equatorial separation at the first division or from genetical or structural causes.

Beadle and McClintock (1928), Beadle (1930, 1932, 1933) in *Zea*, Satina and Blakeslee (1935), Bergner (1935) in *Datura*, Gregory (1905), Fabergé (1937) in *Lathyrus odoratus*, Koller (1938) and Sansome (unpub.) in *Pisum sativum*, describe abnormal meiotic phenomena which are determined by genes and lead to unusual numbers of chromosomes in the gametes. These genes interfere either with chiasma formation, Beadle (1933), Sansome (unpub.), with retention of chiasmata until metaphase, Fabergé (1937), or with cell wall formation, or with normal disjunction by causing the chromosomes to be sticky (Beadle). Low chiasma frequency leading to irregular disjunction is found in some hybrids.

Abnormalities in gametogenesis have been induced by artificial means, such as low temperature and chemical action. The literature on this subject has been reviewed by Winkler (1916). Later experiments and observations have been carried out by Sakamura (1920), Borgenstam (1922), de Mol (1923*a*,*b*), Michaelis (1926), Sakamura and Stow (1926), Stow (1926) and Shimotomai (1927). De Mol for example induced the formation of diploid pollen grains in the hyacinth and obtained triploid progeny by their use on diploid plants.

These cytological abnormalities are sometimes localised upon the plant (*Prunus*, Darlington (1930*a*), *Digitalis*, Buxton and Newton (1928)) and are probably due to environmental influences.

The second type of irregularity, " syndiploidy," does not appear to be directly connected with failure of pairing, or with hybridity, since it occurs, both in hybrids such as *Raphanus-Brassica*, and in non-hybrid material (Maize, Beadle, 1931).

The consequence of syndiploidy is that diploid gametes are produced, or, when in addition, the first division is nullified, dyads of spores are formed each with the tetraploid number of chromosomes.

The third type of abnormality is cytologically distinct from the first type in that the first division is completely suppressed, and not the result of a first division being nullified.

Polyploid gametes, or rather aneuploid gametes, may be formed as a result of further irregularities in the above three main types of abnormal behaviour. For example, in the first type all the chromosomes may not be included in the " restitution nucleus." Each chromosome and its homologue has the potentiality of anomalous behaviour, independently of the remaining chromosomes. Hence, opportunity is given for the production of gametes with more or less than the normal reduced chromosome number.

The genetical consequences resulting from the three types of abnormality are different.

In syndiploidy pairing and disjunction of all or any of the homologous chromosomes can take place, and therefore the resulting nuclei may be different in factor content, from one another and from the original parent. In the two remaining types no heterotype division takes place, or if it does the result of the division is nullified by the inclusion of all the separated chromosomes within one nucleus. Therefore in these two types of abnormality, there is no qualitative change of the chromosome complement from that of the somatic complement of the parent. There may, however, be a quantitative change such as the formation of a tetraploid gamete when the somatic tissue is diploid.

Naturally inference plays a large part in deciding the mode of origin of polyploid gametes. The cytology of the parent will sometimes throw light on this question, but often the decision depends on the behaviour of the succeeding derivative polyploid plants themselves. For this reason there are only a few cases in which the evidence is adequate to decide the exact mode of origin of a special polyploid gamete.

The following are examples of polyploids which have arisen in experimental interspecific hybrid material from hybrid F_1 plants (the hybrid *Raphanus-Brassica* is, of course, intergeneric). We shall divide them into two classes : (*a*) those polyploids which have arisen through the fusion of two unreduced gametes and are fertile, (*b*) those which have resulted from the fusion of an unreduced egg with a normal pollen grain. In interspecific hybrids of *Digitalis*, *Raphanus-Brassica*, *Phleum*, *Nicotiana* and *Fragaria* we have examples of the first class.

Digitalis purpurea ($2n = 56$) × *D. ambigua* ($2n = 56$) gave practically sterile F_1 hybrids ($2n = 56$) and their selfed progeny had double the chromosome number ($2n = 112$) (Buxton and Newton, 1928).

On crossing *Raphanus sativus* ($2n = 18$) with *Brassica oleracea* ($2n = 18$) Karpechenko (1924, 1927*a*,*b*, 1928), obtained hybrids with 18 somatic chromosomes. Most of these hybrids were self-sterile, but a few were slightly fertile and gave an F_2 progeny consisting mainly of tetraploids ($2n = 36$), a few hypertetraploids ($2n = 37$–38) and a few with approximately the hexaploid number ($2n = 54$).

Phleum pratense ($2n = 14$) × *Phleum alpinum* ($2n = 28$) gave almost sterile triploid hybrids ($2n = 21$), but Gregor and Sansome (1930) succeeded in raising a progeny of four plants which were hexaploid ($2n = 42$).

Lammerts (1931) found that most of the F_2 progeny from the triploid hybrid *Nicotiana rustica* ($2n = 48$) × *N. paniculata* ($2n = 24$) were approximately hexaploid with about 72 chromosomes.

By selfing the F_1 hybrid of the cross *Fragaria bracteata* ($2n = 14$) × *F. Helleri* ($2n = 14$) Ichijima (1926, 1930) obtained a tetraploid plant ($2n = 28$).

In all these cases, the respective authors have obtained cytological evidence indicating that the F_1 produces unreduced gametes. It is noteworthy that except for *Fragaria* the F_1 hybrids were more or less sterile. This is largely due to abnormal meioses, leading to the production of unbalanced gametes (see p. 15). Doubling of the chromosome number of these sterile hybrids has resulted in normal meiosis and hence normal fertility. Further, the tetraploids of *Digitalis* and *Raphanus-Brassica* were almost identical morphologically with the diploid hybrids. The tetraploid *Fragaria* breeds approximately true and is probably of the same nature as *Primula Kewensis* in being an allotetraploid with predominant autosyndesis (see p. 198).

In the second class we have *Galeopsis pubescens* ($2n = 16$) × *G. speciosa* ($2n = 16$) which gave highly sterile F_1 plants ($2n = 16$). Six F_2 plants consisted of five diploids and one triploid ($2n = 24$) (Müntzing, 1930*a*). F_1 hybrids of *Salix viminalis* ($2n = 38$) × *S. caprea* ($2n = 38$) were found by Håkansson (1929*a*) to have 38 somatic chromosomes. The F_2 plants were diploids with the exception of two which were heteroploids. One was a triploid ($2n = 57$) and the other was the sterile hypertetraploid ($2n = 82—84$) known as *S. Laurina*. This example is almost identical with that of *Galeopsis*.

Brieger (1928*a*) crossed the tetraploid *Nicotiana Tabacum* ($2n = 48$) with the diploid *N. Rusbyi* ($2n = 24$) and obtained triploid hybrids with 36 chromosomes. The hybrids back-crossed with *N. Tabacum* gave among their progeny one pentaploid ($2n = 60$) and one plant containing approximately 55 chromosomes.

In all these F_1 hybrids irregularities were observed at meiosis, *e.g.*, fusion of the homotypic spindles, giving rise to unreduced gametes so that without doubt these polyploids arose through fertilisation of an unreduced egg with a normal pollen grain. It is probable that 24 of the 55 chromosomes of the *Nicotiana* plant are derived from the male parent *N. Tabacum,* while the remaining 31 are derived from the triploid hybrid.

The following group of polyploids are those which have arisen directly from a cross and they all belong to the class in which an unreduced egg has been fertilised by a normal pollen grain.

Nicotiana Tabacum ($2n = 48$) when crossed with the diploid *N. sylvestris* ($2n = 24$) gave 50 F_1 plants of which 49 were sterile triploids ($2n = 36$) and one was a fertile pentaploid ($2n = 60$) (Webber, 1930*b*). *Nicotiana Tabacum* var. *Dubek* ($2n = 48$) × *N. rustica* (Turkestan var. *Kolmak*) ($2n = 48$) gave two self-sterile hybrids (Eghis, 1927). One of these hybrids TR_1 was found by Rybin (1927) to be a hexaploid ($2n = 72$). TR_1 was fertile when crossed with other varieties of *N. Tabacum* or with varieties of *N. rustica.* TR_1 × *N. rustica* var. *texana* gave five plants, of which one 0156/256 proved to be an octoploid with 96 chromosomes. 0156/256 was self-fertile and like TR_1 was cross fertile with other varieties of *N. Tabacum* and *N. rustica.*

The pollination which gave rise to TR_1 was carried out during cold weather in autumn and that giving rise to 0156/256 just after an abrupt fall in temperature. Low temperature has led to the production of unreduced gametes in *Nicotiana Tabacum* var. *Dubek* and in other species, and it is therefore concluded that this is the explanation of the origin of these polyploid *Nicotiana* plants. From the following evidence it is believed that the extra chromosomes of TR_1 and 0156/256 are derived from the respective female parents. TR_1 shows greater similarity to *N. Tabacum* than the tetraploid hybrids of the reciprocal cross (*i.e.,* $TR_1 = 48T + 24R$).

The sister plants of 0156/256 were intermediate between *N. Tabacum* and *N. rustica,* while 0156/256 resembled *N. rustica* more so than TR_1 (*i.e.,* $0156/256 = 48T + 48R$).

Similar results to those obtained by Eghis and Rybin with their *Nicotiana* hybrids have been found in *Galeopsis.* The triploid hybrid *Galeopsis pubescens-speciosa* ($2n = 24$) previously mentioned, when back-crossed with *G. pubescens* ($2n = 16$) produced a single fertile tetraploid plant ($2n = 32$) (Müntzing, 1930*b*).

Fusion of the homotypic spindles was observed in meiosis of the triploid, thus providing evidence for the production of unreduced gametes. The tetraploid, like the triploid, was morphologically undistinguishable from *G. Tetrahit.* Meiosis was normal and in genetical behaviour like *G. Tetrahit.* It was self-fertile and crossed readily with *G. Tetrahit,* but reciprocal crosses with its ultimate ancestors *G. pubescens* and *G. speciosa* gave no seed. The tetraploid derivative is therefore similar to the Linnean species *G. Tetrahit,* but it has been produced experimentally.

Rubus rusticanus inermis ($2n = 14$) × *R. thyrsiger* ($2n = 28$) gave three hybrid plants referred to as RT_2, RT_3 and RT_4. The first two were sterile triploids ($2n = 21$) while RT_4 was a fertile tetraploid ($2n = 28$) (Crane and Darlington, 1927).

Diploid gamete formation has not been observed in *R. rusticanus,* but it has been seen in a related *Rubus* species. It is believed that the tetraploid RT_4 probably arose by fusion of an unreduced egg of the female diploid parent *R. rusticanus* with a normal diploid pollen-grain of the tetraploid male parent *R. thyrsiger* for the following reasons. The triploid sister plants of RT_4 approached the tetraploid parent in type while RT_4 exhibited four characters which were only shown by the diploid parent (*i.e.,* $RT_4 = 14R + 14T$).

The following polyploids have arisen spontaneously within a diploid species. The first class has presumably arisen from the union of two unreduced gametes. Blakeslee, Belling and Farnham (1923) first discovered a tetraploid *Datura Stramonium* ($2n = 48$) in 1916 among the progeny of the diploid species ($2n = 24$). In 1919 five and possibly six more tetraploids were discovered. Tetraploid forms of *Primula sinensis* ($2n = 48$) were found among a batch of diploid plants by Gregory (1914) and Sömme (1930).

The second class have probably resulted from the fusion of an unreduced egg with a normal pollen grain giving triploids. Among their cultures of *Zea Mays* ($2n = 20$) Randolph and McClintock (1926) found one triploid plant ($2n = 30$). Similarly, Lesley and Lesley (1930) found three triploids ($2n = 36$) amongst about 9,000 normal diploid tomato plants ($2n = 24$). Triploids appear to arise more frequently in progeny of plants with an unbalanced chromosome number since six triploids were found among 2,000 plants in the progeny of trisomic plants (see p. 223).

In the progeny of a plant of *Crepis capillaris* ($2n = 8$) Navashin (1925*b*) found one triploid ($2n = 12$) and one pentaploid ($2n = 20$).

It is difficult to obtain cytological evidence for the production of unreduced gametes in normal diploids since meiosis is generally regular. Further, the comparatively rare occurrence of polyploids indicates how seldom an abnormality occurs in meiosis. In maize cultures, however, a few cases of binuclear microsporocytes containing 20 bivalents at first metaphase have been observed. Low temperature is known to cause the production of unreduced gametes, and this may be the reason for the production of a diploid and tetraploid gamete by the *Crepis* plant which had been grown under abnormal climatic conditions. In *Datura* the fact that most of the tetraploids appeared in one season also makes one suspect a similar environmental cause for the formation of diploid gametes. Moreover, the genetical constitution of the diploid parents and of the tetraploids showed that the reduction division had taken place before the origin of tetraploidy. The possibility of apogamy of a $4x$ egg cell as suggested by Gates (1915) for the origin of tetraploids in *Œnothera* is therefore eliminated and likewise the possibility of apomixis. It appears likely that doubling of the chromosome number in *Datura* happened soon after the reduction division, but there is also the possibility that it took place very early in the zygote.

Darlington (1931*c*) has summarised the pertinent facts regarding the origin of tetraploids in *Primula sinensis*. He points out that the absence of spontaneous triploids as in *Datura*, suggests somatic doubling to be the origin of some tetraploids. The literature key contains a few examples of the origin of polyploidy.

CHAPTER VI

AUTOPOLYPLOIDS

Introduction — Cytology — Characteristics — Segregation — Quantitative Expressions — Linkage.

Introduction. In a polyploid with more than two sets of chromosomes the possibilities at meiosis are more complex than in diploids. If the polyploid is composed of reduplicated sets of the normal diploid complement as in the somatically doubled tetraploid tomato, where the four sets are all homologous, pairing and the consequent disjunction may take place between parts of any two of four homologous chromosomes. This autopolyploid, adopting Kihara and Ono's terminology, differs from an " allopolyploid " where dissimilar sets of chromosomes are included in one plant. The tetraploid *Primula Kewensis* contains two sets of *P. verticillata* and two sets of *P. floribunda* chromosomes, and is therefore an allopolyploid. In autopolyploids only autosyndesis (*i.e.*, pairing of chromosomes of similar sets or descent) can take place, but in allopolyploids both auto- and allosyndesis can occur. For example, in the hybrid between *Papaver striatocarpum* ($2n = 70$) and *P. nudicaule* ($2n = 14$) Ljungdahl (1924) found that 21 bivalents were formed. This is assumed to result from internal pairing among the *striatocarpum* complement (autosyndesis) and pairing of the complement of *nudicaule* with 7 of the *striatocarpum* chromosomes (allosyndesis).

With the discovery of the prevalence of structural changes, the phylogenetical and autosyndetic relationships of chromosomes may not be so well defined as they were thought to be a few years ago. It is possible for example for simple structural changes to isolate chromosomes of a common origin from one another, or by other changes to induce " autosyndesis " in formerly allosyndetically pairing chromosomes. Therefore it is expected and found that all degrees of " homology " are found in polyploids.

In the allotetraploid *Primula Kewensis* the *verticillata* chromosomes generally pair among themselves and the *floribunda* chromosomes do likewise (autosyndesis), but Newton and Pellew (1929) found that occasionally four chromosomes were associated, indicating that two of the *verticillata* and two of the *floribunda* chromosomes had together formed a quadrivalent (allosyndesis). Only autosyndesis occurs in the allopolyploid *Nicotiana digluta* (Clausen and Goodspeed, 1925), which contains two sets of *N. Tabacum* chromosomes and two sets of *N. glutinosa* chromosomes; 24 *Tabacum* bivalents and 12 *glutinosa* bivalents are formed.

These types of pairing—auto- and allosyndesis have a definite effect on the segregation of characters. The genetics of autopolyploids in which only autosyndesis occurs will be dealt with first.

Cytology. The cytology of autotetraploids on which genetical work has been done, is known for *Primula sinensis* (Sömme (1930), Darlington (1931*c*)), *Datura Stramonium* (Belling and Blakeslee (1923, 1924*a*); (Blakeslee, Belling and Farnham (1923)) and *Solanum Lycopersicum* (Jørgensen (1928); Lesley and Lesley, (1930); Upcott, (1935)). Lawrence (1929, 1931*a*) has described the behaviour of the chromosomes in the allo-octoploid *Dahlia variabilis*, which shows tetrasomic inheritance for some characters.

The formation of quadrivalents as well as bivalents at heterotypic metaphase may lead to the occasional production of gametes with more or less than the $2x$ number of chromosomes. Further, instead of one chromosome pairing with another and then disjoining to the opposite pole as in a bivalent (normal disjunction) the formation of a multiple association of four chromosomes will sometimes lead to chromosomes or parts of chromosomes which have paired at prophase going to the same pole at anaphase (non-disjunction) (see p. 15). Non-disjunction in a quadrivalent can give rise to two types of abnormalities in the formation of gametes, both of which affect the heritable constitution of the gametes. Either there may be an unequal numerical distribution of the chromosomes to the gametes, *i.e.*, numerical non-disjunction, (*vide* Darlington, 1931*c*), or genetical non-disjunction where the gametes have the $2x$ number of chromosomes, but some parts of the chromosomes which had paired appear in the same gamete instead of in different gametes.

All the chromosomes of the tetraploid *Datura* may form quadrivalents, but the average for *Primula sinensis* is 10·4 quadrivalents and 3·2 bivalents (Darlington, 1931*c*). Jørgensen (1928) found only one or two quadrivalents in his somatically doubled tomato, but the Lesleys (1930) found 7–12% quadrivalents in a tetraploid tomato raised from seed. Darlington has suggested that the differences in quadrivalent formation between the above genera are due to differences in the frequency of chiasma formation in the species. *Datura* has a higher frequency of chiasma formation than *Primula sinensis.* It is therefore to be expected that more complex multiple associations will be formed in *Datura* than in *Primula sinensis.* This suggestion is supported by the fact that certain complicated configurations of chromosomes which require six chiasmata for their occurrence are found in *Datura* but not in *Primula sinensis.*

A statistical count of chromosome numbers in *Datura* and *Solanum* was made by Blakeslee, Belling and Farnham and the Lesleys, respectively. In *Datura* out of 243 pollen mother-cells examined 70% had the normal 24–24 distribution and 30% had 23–25, while 22–26 and 21–27 were only found rarely. In tomato 23–25 was found in 22% of cases and 22–26 in 6% of cases out of 49 second divisions examined. Jørgensen, on the other hand, found great regularity of the 24—24 distribution in his tomato material. A study of the chromosome numbers in pollen grains of triploid *Hyacinthus* has also been made by Belling and by Darlington (see Darlington, 1926).

Meiosis in *Primula sinensis* was found to be fairly regular (Sömme (1930) ; Darlington (1931*c*)). Non-disjunction of chromosomes was observed and giant cells were sometimes found at the second division. A statistical count of the numbers of chromosomes present at the second division has not been made, but it may be assumed that, as in *Datura,* the amount of numerical non-disjunction will not appreciably affect the genetic results. In the case of *Dahlia variabilis* meiosis and numerical disjunction is remarkably regular.

General Characteristics. The increased vegetative vigour of the tetraploid as compared with the diploid is generally noticeable, but the 4*x* *Primula obconica* (Philp, unpub.) is an exception to this rule.

The tetraploid form of *Primula sinensis* is in every respect a coarser and bigger plant than the diploid form from which it arises but otherwise closely resembles it (Gregory, de Winton and Bateson, 1923). In this respect it differs from the tetraploid *Datura* which has characters not common to the diploid form, such as spherical instead of ovate capsules and broader leaves (Blakeslee, Belling and Farnham, 1923). The tetraploid form of *Campanula persicifolia* has a shallower corolla than the diploid form (Gairdner, 1926), and in *Solanum* Jørgensen (1928) and Sansome (1930) find that the leaf shape of the tetraploid is distinctly different from that of the diploid. Like the tetraploid forms of *Datura* and *Solanum* the tetraploid *P. sinensis* is much less fertile, produces distinctly bigger pollen grains and more bad pollen than the diploid form.

Darlington pointed out in 1928 that there was a correspondence between the fertility of a diploid and its polyploid derivative dependent on the chromosome behaviour.

There is an inverse correlation between the fertility of the diploid and derivative polyploid. Doubling of the chromosome number in a sterile hybrid generally results in a return to fertility in the polyploid. This is because the chromosomes can pair and behave normally in meiosis giving normal gametes. If the diploid, *e.g.*, *P. Kewensis* ($2x$), is made up of two different sets of chromosomes the plant will be practically sterile since the gametes produced will result from the random assortment of chromosomes in an irregular meiosis. When

	Seed production of the Plant with the Lower Chromosome number.	Seed production of Polyploid derivative.
Raphanus-Brassica (Karpechenko, 1927).	45 per plant	30 per pod.
Phleum pratense × *P. alpinum* (Gregor and Sansome, 1930).	46 in 500,000 flowers, 4 germinated.	over 400 per plant, 90% germination.
Digitalis purpurea × *D. ambigua* (Buxton and Newton, 1928).	200 seedlings from 2 plants.	400 per capsule.
Solanum Lycopersicum (Sansome unpublished).	100 per fruit.	20 per fruit.
Datura Stramonium (Blakeslee, Belling and Farnham, 1923).	352 per fruit.	70 per fruit.
Primula sinensis (Sömme, 1930) .	12·6 per fruit.	9·0 per fruit.
Primula sinensis (Darlington, 1931) .	32·2 per fruit.	23·2 per fruit.
Campanula persicifolia (Gairdner and Darlington, 1932).	325 per fruit.	150* per fruit.

* In the original paper the number 130 was given in error.

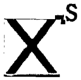
this diploid becomes tetraploid, however, it will be fertile, since autosyndesis will take place and give rise to bivalents at metaphase, with the consequent regular production of viable balanced gametes. *e.g.*, tetraploid *P. Kewensis*. When the diploid is fully fertile the derivative tetraploid will be less fertile, since too much similarity in each group of four chromosomes introduces competition in pairing, therefore non-disjunction will occur, giving rise to unbalanced gametes. The seed production of diploids and tetraploids given above indicates this inverse correlation. This explains why allopolyploids are much more widespread in nature than autopolyploids. Any change which differentiates the chromosomes from one another will lead to bivalent formation (allopolyploidy) and to increase in fertility. Such a change will therefore be favoured by selection (see Müntzing, 1936).

INHERITANCE IN AUTOTETRAPLOIDS

Recently tetraploid inheritance has been studied in *Datura Stramonium*, Blakeslee, Belling and Farnham (1923); *Dahlia variabilis*, Lawrence (1929, 1931*a*); Lawrence and Scott-Moncrieff (1935); *Primula sinensis*, Sömme (1930) and de Winton and Haldane (1931); tomato, Sansome (1933); *Zea Mays*, Randolph (1932). Autotetraploid inheritance with random pairing between four chromosomes, two at a time, followed by regular disjunction to opposite poles of those chromosomes which have paired, gives rise to more complex ratios than in diploids, but (as in diploids) the gametic output obeys the laws of chance and is amenable to mathematical calculation. Muller (1914) and Lawrence (1929) calculated the gametic series to be expected on the above conditions for tetraploids and octoploids. Muller (1914) in considering Gregory's results showed that the assortment of the homologous chromosomes in the autotetraploid must be at random thus leading to a random assortment of factors to the gametes.

Using the accepted terminology of Blakeslee, Belling and Farnham, with respect to one factor S, there are five possible types of zygote in the tetraploid, quadruplex SSSS, triplex SSSs, duplex SSss, simplex Ssss and nulliplex ssss, whereas in the diploid there are only three possible types SS, Ss and ss.

If these factors in the tetraploid are assorted at random two at a time, a duplex plant SSss will have a gametic output of 1SS : 4Ss : 1ss. The possible combinations may be represented diagramatically thus :—



Such a plant on selfing would give a progeny of (1SS 4Ss 1ss)^2 or 1SSSS, 8SSSs, 18SSss, 8Ssss, 1ssss.

TABLE 23

Tetrasomic Inheritance of an Allelomorphic Pair (A, a) in Tetraploid Daturas; Formulae for Parents, Gametes, and Offspring (Blakeslee, Belling and Farnham, 1923).

Parents (Gametes in parentheses).	Mated with	Genetic Types of Offspring.					Ratio $A : a$.
		A_4.	A_3a.	A_2a_2.	Aa_3.	a_4.	
A_4 (A_2)	A_4	1					∞ : 0
	A_3a	1	1				∞ : 0
	A_2a_2	1	4	1			∞ : 0
	Aa_3		1	1			∞ : 0
	a_4			1			∞ : 0
A_3a (A_2+Aa)	A_4	1	1				∞ : 0
	A_3a	1	2	1			∞ : 0
	A_2a_2	1	5	5	1		∞ : 0
	Aa_3		1	2	1		∞ : 0
	a_4			1	1		∞ : 0
A_2a_2 ($A_2+4Aa+a_2$)	A_4	1	4	1			∞ : 0
	A_3a	1	5	5	1		∞ : 0
	A_2a_2	1	8	18	8	1	35 : 1
	Aa_3		1	5	5	1	11 1
	a_4			1	4	1	5 : 1
Aa_3 ($Aa+a_2$)	A_4		1	1			∞ : 0
	A_3a		1	2	1		∞ : 0
	A_2a_2		1	5	5	1	11 : 1
	Aa_3			1	2	1	3 : 1
	a_2				1	1	1 : 1
a_4 (a_2)	A_4			1			∞ : 0
	A_3a			1	1		∞ : 0
	A_2a_2			1	4	1	5 : 1
	Aa_3				1	1	1 : 1
	a_4					1	0 : ∞

Where the dominance of a factor over its allelomorph is complete, *e.g.*, short style over long style in *Primula sinensis*, the phenotypic ratio when a duplex plant is selfed is 35 : 1. Back-crossing such a plant to the recessive will give a ratio of 5 : 1.

Table 23 shows the gametic output and zygotic ratios expected in autotetraploid plants. Considering one factor there is only one heterozygote in a diploid, and when dominance is complete, on selfing or intercrossing and back-crossing, it can only give two phenotypic ratios 3 : 1 and 1 : 1. In an autotetraploid, on the other hand, there are three heterozygotes and five possible phenotypic ratios 35 : 1, 11 : 1, 5 : 1, 3 : 1 and 1 : 1. Consequently, in breeding from heterozygous tetraploids, a much larger progeny must be grown in order to obtain the recessive form as compared with that required to be grown from a heterozygous diploid.

TABLE 24

Tetrasomic Inheritance in the Octoploid Dahlia variabilis (Lawrence, unpublished,)

Cross.	Number of Families.	Theoretical ratio.	Observed.		Calculated.		$\frac{\text{Dev.}}{\sigma}$
			Dominant.	Recessive.	Dominant.	Recessive.	
$A_3a \times a_4$	4	∞A : 0a	180	0	180	0	—
$A_2a_2 \times A_2a_2$	2	35A : 1a	85	1	83·6	2·4	0·91
$A_2a_2 \times a_4$	7	5A : 1a	221	44	220·8	44·2	0·02
$Aa_3 \times a_4$	2	1A : 1a	99	115	107·0	107·0	1·09
$a_4 \times a_4$	47	0A · ∞a	0	2,327	0	2,327	—
B_3b or $B_4 \times B_2b_2$	2	∞B : 0b	72	0	72	0	—
B_3b or $B_4 \times b_4$	1	∞B : 0b	92	0	92	0	—
$B_2b_2 \times b_4$	4	5B : 1b	237	44	234·2	46·8	0·45
$Bb_3 \times B_4$	9	1B : 1b	309	314	311·5	311·5	0·20
$b_4 \times b_4$	46	0B : ∞b	0	2,004	0	2,004	—
$Y_3y \times Y_2y_2$	5	∞Y : 0y	444	0	444	0	—
$Y_3y \times Yy_3$	3	∞Y : 0y	259	0	259	0	—
$Y_3y \times y_4$	4	∞Y : 0y	378	7*	385	0	—
$Y_2y_2 \times Y_2y_2$	1	35Y : 1y	107	3	106·9	3·1	0·02
$Y_2y_2 \times Yy_3$	5	11Y : 1y	513	50	516·1	46·9	0·46
$Y_2y_2 \times y_4$	21	5Y : 1Y	708	169	730·8	146·2	2·11
$Yy_3 \times Yy_3$	7	3Y : 1y	411	118	396·8	132·2	1·42
$Yy_3 \times y_4$	16	1Y : 1y	488	472	480·0	480·0	0·51
$y_4 \times y_4$	14	0Y : ∞y	0	558	0	558	—

* Recessives arising from double reduction.

Haldane (1930*a*) has given a general method for the calculation of the gametic output of any autopolyploid in which the factors are distributed at random to the gametes in the above manner. The

TABLE 25

Cross.	Number of Families.	Theoretical ratio.	Observed. Dominant.	Observed. Recessive.	Calculated. Dominant.	Calculated. Recessive.	$\frac{\text{Dev.}}{\sigma}$
Datura Stramonium							
A_4 or a_3 × A_4 or a_3	9	∞A : oa	1,897 :	0	1,897 :	0	—
A_4 or a_3 × A_2a_2 and reciprocal	5	∞A : oa	439 :	0	439 :	0	—
A_4 or a_3 × A_1a_3	9	∞A : oa	747 :	7	754 :	0	—
A_4 or a_3 × a_4	6	∞A : oa	257 :	6	263	0	—
A_2a_2 × A_2a_2	13	35A : 1a	3,383 :	118	3,403·7 :	97·3	3·15
A_2a_2 × A_1a_3 and reciprocal	6	11A : 1a	319 :	32	321·7 :	29·3	0·77
A_2a_2 × a_4	10	5A : 1a	518 :	137	545·8 :	109·2	4.32
A_1a_3 × A_1a_3	9	3A : 1a	1,337 :	570	1,430·2 :	476·8	7·3
A_1a_3 × a_4	6	1A : 1a	144 :	144	144 :	144	0·00
P_4 or P_3p × P_4 or P_3p	5	∞P : op	1,201 :	0	1,201 :	0	—
P_4 or P_3p × P_2p_2 and reciprocal	3	∞P : op	128 :	0	128 :	0	—
P_4 or P_3p × P_1P_3	1	∞P : op	75 :	0	75 :	0	—
P_4 or P_3p × p_4	6	∞P : op	532 :	0	532 :	0	—
P_3p × P_3p	3	∞P : op	1,280 :	0	1,280 :	0	—
P_3p × p_4 and reciprocal	3	∞P : op	160 :	1	161 :	0	—
P_2p_2 × P_2p_2	80	35P : 1p	9,199 :	225	9,162·8 :	261·8	3·42
P_2p_2 × P_1p_3	9	11P : 1p	394 :	42	339:6 :	36:3	1:46
P_2p_2 × p_4	31	5P : 1p	546 :	122	556:7 :	111·3	1·64
Pp_3 × Pp_3	59	3P : 1p	7,547 :	2,619	7,634·5 :	2,541·5	1·10
Pp_3 × p_4	36	1P : 1p	696 :	682	689 :	689	0·55
Primula sinensis.							
S_2s_2 × s_4	11	5S : 1s	287 :	45	276·7 :	55·3	1·5
S_1s_3 × S_1s_3	28	3S : 1s	1,000 :	342	1,006·5 :	335·5	0·4
S_1s_3 × s_4	36	1S : 1s	1,007 :	995	1,001 :	1,001	0·3
G_2g_2 × G_2g_2	38	35G : 1g	1,659 :	52	1,663·5 :	47·5	0·7
G_2g_2 × g_4	30	5G : 1g	1,175 :	223	1,165 :	233	0·7
G_1g_3 × G_1g_3	9	3G : 1g	172 :	59	173·2 :	57·8	0·4
G_1g_3 × g_4	15	1G : 1g	240 :	212	226 :	226	1·3
B_2b_2 × B_2B_2	5	35B : 1b	205 :	5	204·2 :	3·8	0·3
B_2b_2 × b_4	7	5B : 1b	272 :	48	266·6 :	54·4	0·8
B_1b_3 × B_1b_3	6	3B : 1b	264 :	79	257 :	86	0·9
B_1b_3 × b_4	25	1B : 1b	456 :	449	453·5 :	453·5	0·2

generalised formula for the probability of a zygote $\mathbf{A}^r\mathbf{a}^{2m-r}$ producing a gamete $\mathbf{A}^s\mathbf{a}^{m-s}$, is

$$\frac{(m\,!)^2\,(2m-r)\,!\,r\,!}{(2m)\,!\,(m-s)\,!\,(m-r+s)\,!\,s\,!\,(r-s)\,!}$$

where r is the number of dominant factors in the zygote, s the number in the gamete and m is the total number of factors in the gamete.

Hence the gametic output of a particular zygote is obtained by calculating the frequency of each possible type of gamete produced.

Tables 24, 25, 27, 28 and 29 give the results of experiments with autotetraploids of *Datura Stramonium* and *D. inermis*, *Primula sinensis* and *Dahlia variabilis*. (*Dahlia variabilis* is an octoploid, but behaves like an autotetraploid with regard to the inheritance of the characters investigated.)

The general agreement between the observed and the calculated ratios is close despite the fact that it is probable that the calculations are based on assumptions that are rarely fulfilled. In the case of spineless, **a**, in *Datura stramonium*, of **G** in *Primula sinensis* (de Winton and Haldane, 1935), of **r** in *Lycopersicum esculentum* (Lindstrom, (1932); Sansome, unpub.), and **y** in *Dahlia variabilis* (Lawrence, 1931) there is qualitative evidence of chromatid segregation in which the locus of the gene has divided before segregation. Triplex plants **AAAa** are not expected to give any recessives but **a** plants are found in *Datura stramonium* (see Table 25), and 1–2% **g** plants arose from **GGGg** plants in *Primula sinensis*. It will be remembered that

TABLE 26

Limits of Gametic Segregation in an Autotetraploid

	Chromosome Segregation.	Random Chromatid Segregation.	Complete Equational Separation.
	A **a**	**A** **a**	**A** **a**
Triplex **AAAa** . .	∞ : 0	27 : 1	23 : 1
Duplex **AAaa** . .	5 : 1	11 : 3	7 : 2
Simplex **Aaaa** . .	1 : 1	13 : 15	11 : 13

TABLE 27

Dominant White—Coloured.

Cross.	Observed.					Calculated.					Number of Families
	White and tinged White.	Lavender.		Magenta.	Red.	White and tinged White.	Lavender.		Magenta.	Red.	
		Magenta.	Red.				Magenta.	Red.			
$W_2w_2B_2B_2G_4 \times w_4b_4G_4$	18	57	6	14	4	16·5	55·0	11·0	13·7	2·8	4
$W_2w_2B_2b_2G_4 \times W_2w_2B_2b_2G_4$	351	88	2	7	1	336·9	97·0	2·7	12·1	0·3	9
	White and tinged White.	Lavender.		Full colour.		White and tinged White.	Lavender.		Full colour.		
$W_2w_2B_2b_2G_2g_2 \times W_2w_2B_2b_2G_2g_2$ Expected ratio. 27 : 8 : 1	363 M = 10·0 $\frac{\text{Dev.}}{\text{M}} = 0{\cdot}6$	114 M = 9·2 $\frac{\text{Dev.}}{\text{M}} = 0{\cdot}5$		15 M = 3·7 $\frac{\text{Dev.}}{\text{M}} = 0{\cdot}3$		369·0	109·3		13·7		8
	Tinged White.					Tinged White.					
$W_2w_2B_2b_2G_2g_2 \times w_4b_4g_4$ Expected ratio. 1 : 4 : 1	43 M = 5·3 $\frac{\text{Dev.}}{\text{M}} = 1{\cdot}7$	121 M = 6·8 $\frac{\text{Dev.}}{\text{M}} = 2{\cdot}0$		38 M = 5·3 $\frac{\text{Dev.}}{\text{M}} = 0{\cdot}8$		33·7	134·6		33·7		6

B and G are linked having cross-over percentages of 35·18% on the female side and 34·38% on the male side.

the centromeres divide reductionally at meiosis (see p. 104) and any locus distal to a chiasma may divide equationally in a certain proportion of cases. Muller's theory implies that the whole chromosome divides reductionally at the first division of meiosis. It is, however, shown that separation and disjunction are variable. Therefore the segregation of a gene will vary greatly. In general each gene will segregate in a particular ratio depending on the number of chiasmata between it and the centromere, and on the properties of the chromosome in disjunction. Other influences, structural, genic and environmental will, however, disturb these phenomena. Hence the segregating ratio of a gene in a polyploid

TABLE 28

Normal—" Primrose Queen " Eye

Cross.	Normal Eye, Long style.	Normal Eye, Homostyle.	Primrose Queen Eye, Homostyle.	Number of Families.
	$(Q_4 + Q_3 + Q_2)$	(Q_1q_3)	(q_4)	
$Q_2q_2 \times Q_2q_2$ . . .	158	31	8	14
Expected on a 27 : 8 : 1 basis.	148·5	43·0	5·5	
	M = 6·0	5·8	2·3	
	$\frac{\text{Dev.}}{\text{M}}$ = 1·6	2·1	1·0	
	(Q_2q_2)	(Q_1q_2)	(q_4)	
$Q_2q_2 \times q_4$ . . .	50	38	17	13
Expected on a 1 : 4 : 1 basis.	17·5	70	17·5	
	M = 3·8	4·3	3·8	
	$\frac{\text{Dev.}}{\text{M}}$ = 8·5	7·4	0·1	
$Q_1q_3 \times Q_1q_3$ . . .	35	31	13	5
Expected on a 1 : 2 : 1 basis.	19·8	39·5	19·8	
	M = 3·9	4·4	3·9	
	$\frac{\text{Dev.}}{\text{M}}$ = 3·9	1·5	3·9	
$Q_1q_3 \times q_4$ . . .	8*	40	44	5
Expected on a 1 : 1 basis.	0	46	46	
	M = —	4·8	4·8	
	$\frac{\text{Dev.}}{\text{M}}$ = —	1·3	0·4	

* These eight plants are probably Q_1q_3 overlapping towards the normal condition.

is only an approximation applicable to one set of conditions (Mather, 1935, 1936, 1938). The possible limits on present day theories are set forth in Table 26.

Chromosome segregation depends on complete reductional separation and normal disjunction. It will be obvious that large numbers of plants must be grown to distinguish between ratios of 12 : 12 and 11 : 13 or between 5 : 1 and 3·5 : 1. When large numbers of plants are grown, practical and technical difficulties are increased, therefore quantitative methods do not provide satisfactory evidence for the conditions of segregation of any particular gene.

Primula sinensis. The inheritance of six factors and their allelomorphs has been studied in the tetraploid *Primula sinensis* :

S s	short *vs*. long style.
G g	green *vs*. red stigma.
B b	magenta *vs*. red flowers.
W w	Dominant white *vs*. coloured flower.
Q q	normal *vs*. " Primrose Queen " eye.
P p	palm *vs*. fern leaf.

These factors are also known in the diploid and are inherited in the normal 1 : 1 and 3 : 1 ratios of disomic inheritance.

Tables 25, 27, 28 and 29 summarise the results of the experiments on inheritance of these factors in the tetraploid.

It will be noticed in some cases that in the crosses of the type $\mathbf{A_2a_2} \times \mathbf{a_4}$ and $\mathbf{A_2a_2} \times \mathbf{A_2a_2}$ the expected results are calculated on two theoretical ratios. One ratio is based on the theory that pairing has taken place in an allosyndetic manner : **A** with **a** but not **A** with **A** nor **a** with **a**, followed by random segregation at the second division.

This theory, suggested by Gregory in 1914, gives ratios of 3 : 1 and 15 : 1 respectively. The other ratio is calculated on the assumption that the chromosomes carrying **A** and **a** pair at random and undergo normal disjunction. The observed results agree more closely with this latter expectation.

Quantitative Expression. In this work some light has also been obtained on the question of the quantitative effect of the factors. Only in the cases of **S.s.** (short *vs*. long style) and **G.g.** (green *vs*.

TABLE 29

Palm—Fern Leaf

Cross.		Palm.	Extra Lobes.	Fern.	Number of Families.
$P_2p_2 \times P_2p_2$	Observed	293	74	10	9
	Expected on a 27 : 8 : 1 basis.	282·7	83·8	10·5	
		M = 8·4	7·9	3·2	
		$\frac{\text{Dev.}}{\text{M}}$ = 1·2	1·2	0·1	
$P_2p_2 \times p_4$	Observed	27	49	18	6
	Expected on a 1 : 4 : 1 basis.	15·7	62·6	15·7	
		M = 3·6	3·8	3·6	
		$\frac{\text{Dev.}}{\text{M}}$ = 3·1	3·6	0·6	
$P_1p_3 \times P_1p_3$	Observed	92	149	76	15
	Expected on a 1 : 2 : 1 basis.	79·3	158·5	79·3	
		M = 7·7	8·9	7·7	
		$\frac{\text{Dev.}}{\text{M}}$ = 1·6	1·1	0·4	
$P_1p_3 \times p_4$	Observed	6*	101	100	10
	Expected on a 1 : 1 basis.	—	103·1	103·1	
		M = —	7·2	7·2	
		$\frac{\text{Dev.}}{\text{M}}$ = —	0·3	0·5	

* These six plants are assumed to be P_1p_3 overlapping to the normal type.

red stigma) was dominance found to be complete, *i.e.*, the simplex form had the phenotypic characteristics of the dominant factor. In the other factors in tetraploid *P. sinensis* the simplex form was only partially dominant in the phenotypic expression, which was intermediate and highly variable. (In diploids S, G, B, Q and P are completely dominant.)

The simplex form (G_1g_3) has a green stigma but the flower colour is almost as dark as that of the nulliplex form (g_4). This is in contrast to the duplex (G_2g_2) and triplex form (G_3g_1) where the flower colour is lighter. Thus it is concluded that G_1 is dominant over g_3 with respect to stigma colour and is only partially dominant in respect of its effect on flower colour.

Of particular interest is the recessive character "Primrose

Queen " eye. The factor for this was found by Gregory (1911) to be in diploids the lowest member of a series of three multiple allelomorphs, viz., " Queen Alexandra " eye (no eye) (Q_1), normal eye (Q) and " Primrose Queen " eye (the eye extends over about a third to a half of the petal) (q). The recessive factor for " Primrose Queen " not only affects the eye but also the style. Gregory found in diploids that this factor caused genetically long-styled plants to become homostyled and that the single dose of the dominant factor (Q) was completely dominant both as regards the effect on the eye and the long style. In tetraploids, however, Q_1 was found to be completely dominant over q_3 regarding the expression of the eye but not as regards the style, *i.e.*, normal eye—homostyled plants were found to be Q_1q_3. These heterozygotes were liable to vary in expression of the style, especially at the latter part of the flowering season. At that time flowers were produced which were normal-eye long-styled. This is therefore not only an example of the quantitative effect of the factors, but also of the effect of one factor on more than one character.

An interesting example of interaction of factors is afforded by the factors for dominant white (**W**) and green stigma (**G**). Flowers with a green stigma (**G**) are paler in colour than those with a red stigma (**g**). The effect of **W** is that of inhibiting the production of flower colour in the peripheral parts of the flower. In the presence of **G**, **WW** causes the flower to be white, while **Ww** inhibits colour in the periphery (*i.e.*, there is a tinge of colour round the corolla tube). In the presence of **g**, **WW** allows a dark flush of colour to be produced round the corolla tube (*var.* Duchess) and **Ww** permits this colour to be diffuse (*var.* General Buller).

In tetraploids there is an increased number of possible combinations of these factors and their interaction and quantitative effects have proved to be troublesome in the classification of the different types of plants. For that reason Table 27 only shows that most of the expected classes have appeared. This condition, as expected, is by no means uncommon in tetraploids, and in one family a range of the phenotypes may be obtained which defies determination of the genotype from the phenotype. Further breeding tests will only reveal the genotype and this process, because of the tetraploid nature of the plants, necessitates the growing of very large progenies, which in many cases is impracticable. In contrast diploids have only three possible genotypes with regard to one pair of factors, and therefore, even when the factor expression differs quantitatively and factor interaction takes place, the possible range of types is less than that in tetraploids. Thus it is seldom necessary to classify diploids by breeding tests. Obviously from a horticultural point of view a much greater number of forms should be obtained from a tetraploid species than from the corresponding diploid species.

A striking example of the quantitative effect of factors was obtained by Lawrence and Scott-Moncrieff (1935) in *Dahlia variabilis*, an allo-octoploid with autotetraploid inheritance of **A B**, two factors for anthocyanin, and **Y** (yellow) **I** (ivory), two factors for flavones. In the progeny of a cross between two parents of known constitution there were 8 yellow, 8 ivory and 0 white-flowered plants when there should have been :—

Yellow.	*Ivory.*	*White.*
6YI 2Yi	6yI	2yi

On testing for flavone the following result was found :—

	Yellow-ivory.	*Yellow-white.*	*Ivory.*	*White.*
expected	6	2	6	2
observed	1	7	8	0

Such a result cannot be due to chance. Three of the seven yellow flowers with a white ground gave a faint positive reaction for ivory flavone (I) while the other four were negative. From these and other results Lawrence concludes that in the presence of **Y** the **I** factors

TABLE 30

Capsule Volume of Funaria hygrometrica (Wettstein, 1924)

diploid	BB 185·62 (50)	—	—	B × b 97·06 (18)	—	—	bb 57·74 (50)
triploid	BBB 176·91 (5)	—	BB × b 145·77 (12)	—	bb × B 101·31 (14)	124·96 (6) qB × qq	bbb 59·62 (17)
tetra-ploid	BBBB 242·71 (50)	BB × Bb 228·18 (8)	—	BB × bb 196·64 (9) Bb × Bb 208·92 (50)	—	—	bbbb 151·35 (50)

cannot exert their full effect. The three yellow-white forms which gave a faint positive reaction for **I**, were probably I_2i_2 in constitution while the other four were Ii_3. The single **YI** form was probably I_3i. It is possible that the material from which the yellow and ivory flavones are manufactured is limited in amount and the **Y** factors obtain a monopoly. **Y** and **I** also interfere with the expression of anthocyanin by the **A** and **B** factors.

This interaction of the chemical processes involved sometimes has a disturbing effect upon the ratios and creates difficulty in genetical analysis.

Tables 30 and 31 of capsule volume and form of polyploid *Funaria hygrometrica* (Wettstein, 1924*a*) illustrate well the influence of a size factor **B** upon character expression. The diploid **Bb** is intermediate between **BB** and **bb**. **BBb, BBbb** and **Bbb** have capsule volumes corresponding to the effect of **B** alone. The nulliplex tetraploid **bbbb** however has a larger volume than expected from the remaining figures. **B** also affects the gametophytic leaf shape, and here the effect of **B** is greater than that of **b**, the leaf areas of **BB** plants being 1·91, **bb** 2·88, **Bb** 2·27.

TABLE 31

Form of Capsule Lid, Breadth/Length

diploid	BB 4·80	—	—	B × b 2·99	—	—	bb 2 63
triploid	BBB 4·52	—	BB × b 3·97	—	bb × B 2·91	—	bbb 2·71
tetra-ploid	BBBB 5·29	BB × Bb 5·13	—	BB × bb 3·04 Bb × Bb 2·75	—	bb × Bb 2·59	bbbb 2·68

Capsule Colour. *Funaria hygrometrica* (Wettstein 1934*a*)

CC	**Cc**	**cc**
orange	yellow-orange	ochre
lid	*lid*	*lid*
orange	red-ochre	ochre

CCC	**CCc**	**ccC**	**ccc**
orange-red	orange	ochre to rusty	ochre
lid	*lid*	*lid*	*lid*
red	dark orange	ochre	ochre

CCCC	**CCCc**	**CCcc**	**Cccc**	**cccc**
orange-black-red		yellow-orange	rust-ochre	rusty
lid		*lid*	*lid*	*lid*
black-red		black-red	ochre	ochre

As regards capsule volume, the full effect of **B** is not reached even in quadruplex tetraploid, but in the case of **C** for colour of capsule the saturation point is reached between 2–3 **C** factors, since **CCCC CCCc** and **CCcc** have all black-red capsule lids while **CC** and **CCc** have dark orange lids. It will be noticed, however, that not until the triplex condition is reached does the general capsule colour become dark red, although the lid does so with **CCcc**.

In the above cases of capsule volume and colour the nulliplex **xxxx** does not resemble the **xx** or **xxx** forms but agrees more with the simplex **Xxxx** or even duplex **XXxx**.

Stern (1928), by means of duplications, was able to breed flies of *Drosophila melanogaster* with increasing numbers of the recessive bobbed genes. Bobbed (**bb**) in the diploid state suppresses the development of hairs on the body of the flies.

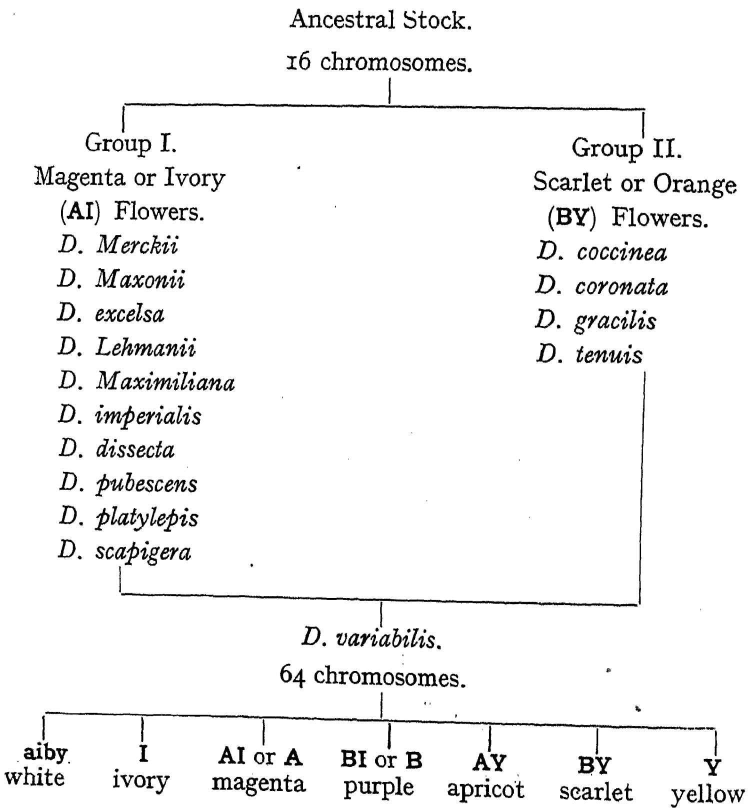
By numerous crosses using duplications of **bb** and its allelomorphs, + normal, $\mathbf{bb}^{l}$ a lethal with more intensive effect, and $\mathbf{bb}^{ll}$, another lethal, Stern was able to show that there was a quantitative effect of these factors upon the development of hairs. To the factors he gives the following numbers as a comparative measure of their influence.

normal	30
$\mathbf{Y}^{bb^{l}}$	10
$\mathbf{X}^{bb}$	8
$\mathbf{Y}^{bb^{ll}}$	4
$\mathbf{X}^{bb^{l}}$	2

When the sum of the values of these allelomorphs present in females amounts to 30, the character of hairs is equal to normal, but when less than 30 the bobbed characteristic, *e.g.*, $\mathbf{X}^{bb}$, $\mathbf{X}^{bb}$, $\mathbf{Y}^{bb^1}$ =26 makes its appearance. The factors on other chromosomes also affect the expression of the bobbed factors. This is shown by the fact that a diploid female with $\mathbf{X}^{bb}$ $\mathbf{X}^{bb}$ has longer hairs than an intersex with more autosomes than normal.

Dahlia variabilis. The octoploid *Dahlia variabilis*, Lawrence and Scott-Moncrieff (1935) combines two groups of flower colour forms only found separately in other *Dahlia* species (see Table 32). Group I has magenta or ivory flowers; the pigments are light in intensity and

TABLE 32 (*after Lawrence*)



consist of an ivory flavone apigenin, and a glucoside of cyanidin. Group II has scarlet or yellow flowers; the pigments are heavy in intensity, and consist of a yellow flavone and an anthocyanin of pelargonidin type. Two anthocyanin genes **A** and **B**, and two flavone genes **I** and **Y**, determine the production of pigment and are inherited in a tetrasomic manner. The expression of the four genes, however, is differential. **Y** and **B** are completely dominant, simplex **Iiii** may not easily be distinguished from nulliplex $\mathbf{i}_4$, but duplex $\mathbf{I}_2\mathbf{i}_2$ is similar to $\mathbf{I}_4$. **Y** may inhibit the action of **I** and **A**, and **YI** may completely suppress the action of **B**. **I** interferes with the action of **A** and may reduce the intense pigmentation of **B** to a light pigmentation. Although **B** and **Y** are completely dominant, and $\mathbf{I}_2\mathbf{i}_2$ is similar to the quadruplex, it may be shown that in all genes the quadruplex, triplex, duplex and simplex, conditions differ in their effect upon the production of colour. For example, $\mathbf{A}_2\mathbf{a}_2\mathbf{I}_4$ does not show anthocyanin pigmentation while $\mathbf{A}_2\mathbf{a}_2\mathbf{I}_3\mathbf{i}$ and $\mathbf{A}_1\mathbf{a}_3\mathbf{I}_2\mathbf{i}_2$ do, although, in the absence of **I**, $\mathbf{A}_1$ and $\mathbf{A}_4$ are indistinguishable.

Lawrence and Scott-Moncrieff suggest that these genes compete for a common source of material from which to build their respective products. The interaction effects show that the genes have different potencies in this competition, **B** and **Y** being very much more effective than **A** and **I**. Whenever more than one **B** gene, or one **B** and a sufficient number of **A** and **I** genes are present, pelargonidin is produced. If fewer potent genes are present, only cyanidin is formed.

Linkage in Autotetraploids. Linkage in polyploids has been investigated in triploid *Drosophila* and maize, and in tetraploid *Primula sinensis* and tomato. With the number of homologous chromosomes greater than two in the sporocytes, greater variation in the assortment of linked factors is to be expected. For example, in a tetraploid with four homologous chromosomes containing two pairs of allelomorphic factors, there are thirteen possible types of arrangement of the factors on the chromosomes (Sömme (1930), de Winton and Haldane (1931), and Sansome (1933)). If we designate the homologous chromosomes by *ABCD* and the factor pairs by **XxYy** we can have the following different arrangements:—

	A	*B*	*C*	*D*	
(1)	**XY**	**xy**	**xy**	**xy**	single coupling.
(2)	**Xy**	**xY**	**xy**	**xy**	single repulsion.
(3)	**Xy**	**Xy**	**xY**	**xY**	double repulsion.
(4)	**XY**	**XY**	**xy**	**xy**	double coupling.
(5)	**XY**	**XY**	**Xy**	**xy**	asymmetrical coupling.
(6)	**xY**	**Xy**	**Xy**	**xy**	asymmetrical repulsion.
(7)	**Xy**	**xY**	**XY**	**xy**	coupling and repulsion.
(8)	**XY**	**Xy**	**Xy**	**xy**	triplex single coupling.
(9)	**Xy**	**Xy**	**Xy**	**xY**	,, ,, repulsion.
(10)	**XY**	**XY**	**Xy**	**xy**	,, double coupling.
(11)	**Xy**	**Xy**	**XY**	**xY**	,, ,, repulsion.
(12)	**Xy**	**XY**	**XY**	**xy**	,, coupling.
(13)	**Xy**	**XY**	**XY**	**xY**	,, repulsion.

Since crossing-over occurs during the time the chromosomes are paired, the method of pairing of the four chromosomes, two at a time, must be considered. With random pairing there are three ways in which these chromosomes *ABCD* can pair, namely, *A* with *B*, *A* with *C* and *A* with *D*, when in each case, of course, the remaining two chromosomes pair with one another. Disjunction of the chromosomes which have paired therefore leads to six possible different types of gametes with respect to chromosome content—*AB*, *AC*, *AD*, *CD*, *BD* and *BC*.

Thus *AC*
| gives the gametes *AC*, *BD*, *AD*, *BC*.
BD

AB
| ,, ,, ,, *AB*, *CD*, *AD*, *BC*.
CD

AB
| ,, ,, ,, *AB*, *CD*, *AC*, *BD*.
DC

To consider the effect of crossing-over, let us take the case of single repulsion. Assuming that chromosome *A* contains the factors **X** and **y**, and that chromosome *B* contains the factors **x** and **Y**, then chromosomes *C* and *D* each contain the factors **x** and **y**. In one, third of all the cases *A* will pair with *B* and if crossing-over takes place between these factors the gametic series with regard to chromosomes *A* and *B* will be $p\ \mathbf{XY} : (1\text{-}p)\mathbf{Xy} : (1\text{-}p)\mathbf{xY} : p\ \mathbf{xy}$ where p is the cross-over value. (This is the same as in diploids.) Chromosomes *C* and *D* will pair and disjoin at the same time as chromosomes *A* and *B*. Crossing-over between *C* and *D*, however, will have no genetical effect since they only contain the recessive factors **xy** and the gametic series with regard to these two chromosomes will be $1\ \mathbf{xy} : 1\ \mathbf{xy}$. In each type of gamete containing an *A* or *B* chromosome there will be a *C* or *D* chromosome, since two chromosomes which have paired do not normally enter the same gamete. Thus considering all four chromosomes the gametic series will be :—

$$p\,\frac{\mathbf{XY}}{\mathbf{xy}} : (1-p)\,\frac{\mathbf{Xy}}{\mathbf{xy}} : (1-p)\,\frac{\mathbf{xY}}{\mathbf{xy}} : p\,\frac{\mathbf{xy}}{\mathbf{xy}}$$

In the remaining two-thirds of cases *A* will pair with *C* or *D* and *B* with *D* or *C*, and in each case crossing-over will have no genetical effect. For each type of pairing the gametic series will be :—

$$\tfrac{1}{2}\,\frac{\mathbf{Xy}}{\mathbf{xy}} : \tfrac{1}{2}\,\frac{\mathbf{Xy}}{\mathbf{xy}} : \tfrac{1}{2}\,\frac{\mathbf{xY}}{\mathbf{xy}} : \tfrac{1}{2}\,\frac{\mathbf{xy}}{\mathbf{xy}}$$

and adding them we get

$$1\,\frac{\mathbf{Xy}}{\mathbf{xy}} : 1\,\frac{\mathbf{Xy}}{\mathbf{xy}} : 1\,\frac{\mathbf{xY}}{\mathbf{xy}} : 1\,\frac{\mathbf{xy}}{\mathbf{xy}}$$

This summed with

$$p\,\frac{\mathbf{XY}}{\mathbf{xy}} : (1-p)\,\frac{\mathbf{Xy}}{\mathbf{xy}} : (1-p)\,\frac{\mathbf{xY}}{\mathbf{xy}} : p\,\frac{\mathbf{xy}}{\mathbf{xy}}$$

gives the total gametic series

$$1\,\frac{\mathbf{Xy}}{\mathbf{xY}} : p\,\frac{\mathbf{XY}}{\mathbf{xy}} : (2-p)\,\frac{\mathbf{Xy}}{\mathbf{xy}} : (2-p)\,\frac{\mathbf{xY}}{\mathbf{xy}} : (1+p)\,\frac{\mathbf{xy}}{\mathbf{xy}}.$$

When dominance is complete the different types of zygote, quadruplex, triplex, duplex and simplex, will be phenotypically indistinguishable. The gametic series may therefore be written $(1+p)\,\mathbf{XY} : (2-p)\,\mathbf{Xy} : (2-p)\,\mathbf{xY} : (1+p)\,\mathbf{xy}$. If p and q represent the cross-over values on the male and female sides respectively, then the zygotic series is :—

$$18+(1+p)(1+q)\,\mathbf{XY} : 9-(1+p)(1+q)\,\mathbf{Xy} :$$
$$9-(1+p)(1+q)\,\mathbf{xY} : (1+p)(1+q)\,\mathbf{xy}.$$

TABLE 33

(de Winton and Haldane, 1931)

Type of Zygote.	Types of Gametes.	Gametes in general.	Gametes, $p=0$.	Gametes $p=\frac{1}{2}$.	Gametes in absence of linkage.	Zygotic ratio on Selfing.
1. **XY.(xy)**$_3$	**XY**	$1-p$	1	1	1	$2+(1-p)(1-q)$
	Xy	p	0	1	1	$1-(1-p)(1-q)$
	xY	p	0	1	1	$1-(1-p)(1-q)$
	xy	$1-p$	1	1	1	$(1-p)(1-q)$
2. **Xy.xY.** **(xy)**$_2$	**XY**	$1+p$	1	1	1	$18+(1+p)(1+q)$
	Xy	$2-p$	2	1	1	$9-(1+p)(1+q)$
	xY	$2-p$	2	1	1	$9-(1+p)(1+q)$
	xy	$1+p$	1	1	1	$(1+p)(1+q)$
3. **XY.Xy.** **(xy)**$_2$	**XY**	$3-p$	3	5	5	$26+(1-p)(1-q)$
	Xy	$2+p$	2	5	5	$9-(1-p)(1-q)$
	xY	p	0	1	1	$1-(1-p)(1-q)$
	xy	$1-p$	1	1	1	$(1-p)(1-q)$
4. **(Xy)**$_2$**.xY.** **xy**	**XY**	$2+p$	2	5	5	$26+pq$
	Xy	$3-p$	3	5	5	$9-pq$
	xY	$1-p$	1	1	1	$1-pq$
	xy	p	0	1	1	pq
5. **(XY)**$_2$**.** **(xy)**$_2$	**XY**	$5-2p+p^2$	5	17	25	$34+(1-p)^2(1-q)^2$
	Xy	$2p-p^2$	0	3	5	$1-(1-p)^2(1-q)^2$
	xY	$2p-p^2$	0	3	5	$1-(1-p)^2(1-q)^2$
	xy	$1-2p+p^2$	1	1	1	$(1-p)^2(1-q)^2$
6. **(Xy)**$_2$**.** **(xY)**$_2$	**XY**	$4+p^2$	4	17	25	$34+p^2q^2$
	Xy	$1-p^2$	1	3	5	$1-p^2q^2$
	xY	$1-p^2$	1	3	5	$1-p^2q^2$
	xy	p^2	0	1	1	p^2q^2
7. **XY.Xy.** **xY.xy**	**XY**	$8+p-p^2$	4	33	25	$136+pq(1-p)(1-q)$
	Xy	$2-p+p^2$	1	7	5	$4-pq(1-p)(1-q)$
	xY	$2-p+p^2$	1	7	5	$4-pq(1-p)(1-q)$
	xy	$p-p^2$	0	1	1	$pq(1-p)(1-q)$

For purposes of calculation it is convenient to put $1-p=P$, $1-q=Q$. The gametic series in double coupling may then be written $4+P^2 : 1-P^2 : 1-P^2 : P^2$, and the expressions for the following zygotic series may be simplified :

Single coupling, $2+PQ : 1-PQ : 1-PQ : PQ$.
Asymmetrical coupling, $26+PQ : 9-PQ : 1-PQ : PQ$.
Double coupling, $34+P^2Q^2 : 1-P^2Q^2 : 1-P^2Q^2 : P^2Q^2$.
Coupling and repulsion, $136+pqPQ : 4-pqPQ : 4-pqPQ : pqPQ$.

The effect of crossing-over in the types 2–7 may be calculated in a similar fashion and the results are given in Table 33, which is taken from the paper by de Winton and Haldane (1931).

It will be observed that in the cases of double coupling, double repulsion and asymmetrical coupling and repulsion a difference in ratio is to be expected between independent segregation of the factors and 50% of crossing-over. In the diploid and in the other types of linkage in tetraploids, this difference is not observable. This fact may be useful, on some occasions, to decide whether two factors are far apart on the same chromosome or on different non-homologous chromosomes.

TABLE 34

Linkage with Random Chromatid Segregation

	XY	xY	Xy	xy
Single coupling .	$2\cdot6-p$	p	p	$3-p$
,, repulsion .	$1+p$	$2\cdot25-p$	$2\cdot25p$	$1\cdot5+p$
Asymmetrical coupling .	$13-2p$	$7+2p$	$2p$	$6-2p$
Double coupling .	$33-6p+p^2$	$6p-p^2$	$6p-p^2$	$9-6p+p^2$

Linkage with only Equational Separation

	XY	xY	Xy	xy
Single coupling .	$11-10p$	$10p$	$8p$	$13-8p$
Single repulsion .	$10+3p$	$23-3p$	$23-6p$	$16+6p$

It will be realised that several assumptions have been made for these calculations. It is assumed that (1) chromatid segregation does not take place; (2) non-disjunction of chromosomes does not occur; (3) only two chromosomes and not chromatids are involved in crossing-over between the genes concerned. It is probable (see previously) that none of these assumptions are true (Sansome, 1933). Mather (1936) has provided a general method in which the amounts of equational separation, non-disjunction and progressive crossing-over may be estimated and allowed for in calculating linkage results in autotetraploids. Using this formula it is of distinct interest that the amount of non-disjunctional and equational separation of **d**, **p**

TABLE 35

Linkage Results in Tetraploid Primula sinensis. (*After de Winton and Haldane,* 1931)

Cross.		Number of Families.	SG	Sg	sG	sg
SINGLE COUPLING.						
$SG.(sg)_3$	$\times (sg)_4$	17	204	126	113	193
	Calculated	—	198·5	119·5	119·5	198·5
$(sg)_4$	$\times SG.(sg)_3$	20	132	89	97	160
	Calculated	—	146	93	93	146
$SG.(sg)_3$	$\times SG.(sg)_3$	7	179	47	40	27
	Calculated	—	174·4	45·3	45·3	27·9
SINGLE REPULSION						
$Sg.sG.(sg)_2$	$\times (sg)_4$	23	126	136	146	102
	Calculated	—	116·9	138·1	138·1	116·9
$(sg)_4$	$\times Sg.sG.(sg)_2$	14	38	57	60	52
	Calculated	—	47·9	55·6	55·6	47·9
DOUBLE REPULSION.						
$(Sg)_2.(sG)_2$	$\times (sg)_4$	12	124	21	19	0
	Calculated	—	113·3	23·4	23·4	3·9
$(sg)_4$	$\times (Sg)_2.(sG)_2$	2	11	0	1	0
	Calculated	—	8·3	1·7	1·7	0·30
DOUBLE COUPLING.						
$(SG)_2.(sg)_2$	$\times (sg)_4$	6	146	18	13	18
	Calculated	—	142·7	19·8	19·8	12·7
$(sg)_4$	$\times (SG)_2.(sg)_2$	2	81	13	9	17
	Calculated	—	87·5	12·5	12·5	7·5
$(SG)_2.(sg)_2$	$\times (SG)_2.(sg)_2$	4	104	3	4	2
	Calculated	—	107·2	2·7	2·7	0·45
ASYMMETRICAL COUPLING.						
$SG.Sg.(sg)_2$	$\times (sg)_4$	3	26	15	3	5
	Calculated	—	21·4	19·4	3·1	5·1
$SG.sG.(sg)_2$	$\times (sg)_4$	14	156	9	108	35
	Calculated	—	134·7	19·3	122	32
$(sg)_4$	$\times SG.sG.(sg)_2$	5	48	7	50	13
	Calculated	—	51·4	7·7	47	12
$SG.sG.(sg)_2$	$\times SG.sG.(sg)_2$	10	373	7	118	10
	Calculated	—	371·2	9·8	121·6	5·4
ASYMMETRICAL REPULSION.						
$Sg.(sG)_2.sg$	$\times (sg)_4$	44	422	98	439	70
	Calculated	—	407·5	107	450	64·5
$(sg)_4$	$\times Sg.(sG)_2.sg$	10	33	7	38	4
	Calculated	—	32·7	8·3	35·7	5·3
$Sg.(sG)_2.sg$	$\times Sg.(sG)_2.sg$	25	847	31	267	7
	Calculated	—	836·8	27·2	283·2	4·8

and s on chromosome 1 of *Lycopersicum esculentum* differs very considerably in duplex and simplex plants. Preferential pairing or segregation as found by Sturtevant (1935) in *Drosophila melanogaster* may be present to further complicate the issue. In many cases " the estimation of the linkage value is little more than a mental exercise " (Sansome, 1933).

The assumption of the purity of the gamete requires to be modified in polyploid inheritance. In tetraploids the gametes are diploid and contain two allelomorphs. For example, a duplex plant S_2s_2 produces gametes of the constitution SS, ss and Ss ; the last type is heterozygous and " impure." The possibility of obtaining pure lines for several characters in the dominant condition is more remote in tetraploids than in diploids. Artificial or natural selection on a diploid with incomplete dominance comparatively soon effects purity, but in a polyploid the recessives are more protected from the action of selection.

CHAPTER VII

ALLOPOLYPLOIDS

Autosyndesis and Allosyndesis — Segregation — Shift — Inheritance in oats and wheat—Speltoids, fatuoids—Evolution and Allopolyploids.

In an autotetraploid the four homologous chromosomes can pair with one another and assort at random to each pole. This type of pairing—autosyndesis—leads to a definite type of segregation of the heritable characters, which has already been dealt with.

Allopolyploids contain a complement of chromosomes derived from two or more plants of dissimilar origin, and it is upon the degree of similarity between these two or more kinds that the type of pairing and disjunction of the chromosomes and hence the segregation of factors depend.

Autosyndesis and Allosyndesis. Two types of pairing of the chromosomes at meiosis in allopolyploids can take place, namely, autosyndetic and allosyndetic. Thus in an allotetraploid there may be two sets of chromosomes derived from one species and two sets of chromosomes derived from a different species. For simplicity we shall consider only one pair of the corresponding chromosomes from each species and designate then *AA BB*.

If *A* is homologous with *A* and *B* with *B*, and if the *A* chromosomes are not homologous with the *B* chromosomes, then *A* will always pair with *A*, and *B* with *B* to form bivalents at meiosis—autosyndesis.

Allosyndesis takes place if the chromosome *A* pairs with the *B*, *i.e.*, allosyndetic pairing between chromosomes of different phylogeny. Obviously there is sometimes difficulty in deciding whether allosyndesis or autosyndesis is taking place in border line cases—the difficulty arises from the factorial constitution (heterozygosity) and the systematic position of the parental species.

Genetical Consequences. Theoretically the genetical results from autosyndesis and allosyndesis will be different. In the former where *A* pairs with *A* and *B* with *B*, the gametes will contain *AB*. The succeeding generation will contain *AABB* like the parent and will behave like a diploid regarding the segregation of single factors. Allosyndesis, on the other hand, will give a gametic output of 1*AA* : 2*AB* : 1*BB*, and consequently a greater range in the chromosomal constitution of the progeny. By such a method of pairing the parental type *AABB* will be recovered only 1 in 16 times on selfing such a plant—the chromosomes behave in separation like the segregation of two factors.

With constant autosyndesis segregation of factors only occurs when the ultimate parent was heterozygous. It follows, therefore, that forms with constant autosyndesis will generally breed true.

In the intergeneric F_1 hybrid ($2n = 18$) between *Raphanus* and *Brassica*, Karpechenko (1927*a*,*b*, 1928) the nine *Raphanus* chromosomes are greatly differentiated from the nine *Brassica* chromosomes. No pairing takes place between the two sets. The F_2 tetraploids which result from the fusion of unreduced gametes (p. 168), are perfectly fertile and breed true. The F_2 plants are of the constitution RRBB where R and B represent the *Raphanus* and *Brassica* sets of chromosomes respectively. Autosyndetic pairing takes place and only gametes of the constitution RB are formed. Some of the plants in the parental species were heterozygous, and Karpechenko found that in the tetraploid offspring segregation took place for those factors in which either the *Brassica* or *Raphanus* species were heterozygous.

Allopolyploids, in which autosyndesis is the prevalent method of pairing, are of widespread occurrence. Difficulty is experienced sometimes in identifying them as polyploids and not as normal diploids. The methods of attacking the problem resolve themselves into two main systems ; one is of a genetical nature, and the other cytological. Comparison with related forms often provides an indication that a form under investigation is an allopolyploid. The related species of commercial wheat and oats may have chromosome numbers of 14, 28 or 42, while the commercial stocks have 42 chromosomes in the somatic cells. This indicates that the cultivated varieties are hexaploids ($6x = 42$). Bivalents are formed at meiosis and their breeding behaviour is like that of a diploid with peculiar complications such as the presence of polymeric and duplicate factors and with the production of off-type forms in an unusual manner (fatuoids and speltoids, see p. 212). It is interesting to note in passing that Gregor and Sansome have synthesised an artificial hexaploid *Phleum* (see p. 342), the origin of which in some respects is presumably analogous to that of the commercial wheat and oats. *Spartina Townsendii* is another species in the Gramineæ which in some degree resembles the above forms as to its mode of origin.

Spartina Townsendii is an allopolyploid which has originated in nature. From its characters it is concluded that it arose by hybridisation of the species *S. alterniflora* and *S. stricta.* Huskins (1930) finds that the somatic chromosome number of *S. alterniflora* is 70, that of *S. stricta* is 56, while that of *S. Townsendii* is 126. He also finds that bivalents are formed in meiosis of *S. Townsendii.* This species is very vigorous, fertile, and breeds practically true. It is therefore concluded that *S. Townsendii* is an allopolyploid hybrid analogous to *Primula Kewensis,* having arisen through doubling of the chromosome number of a sterile hybrid between *S. alterniflora* and *S. stricta.* The formation of bivalents and its true breeding nature indicate that autosyndesis takes place.

Besides being important from the evolutionary standpoint by producing a new true breeding form by inter-crossing two species whose chromosomes are non-homologous, the process of autosyndesis enables a number of valuable physiological properties, dependent upon heterozygosity, to be retained. Polymeric factors are characteristic of allopolyploids (see p. 206). If two species hybridise they will probably be somewhat closely related and will have similar factors in common. The polyploid hybrid will contain these factors and they will segregate independently of one another. One can visualise the position where one pair of factors is heterozygous and the other pair is dominant and homozygous for the same character. The segregation of the heterozygous pair in the polyploid will not affect the particular character expression, since it will be controlled by the other pair of dominants. Hence an allopolyploid may be heterozygous for several factors and yet on account of autosyndesis breed true. It is well known that heterozygosity is often accompanied by increased vigour (so-called hybrid vigour

The work of Biffen (1916), while illustrating shift, also shows how such a type of pairing may persist with extreme regularity. In the progeny of a grey-chaffed Rivet, *Triticum turgidum*, crossed with a white-chaffed *T. polonicum*, he found no segregation in chaff colour. From 20 F_1 plants succeeding generations were grown up to F_6 totalling almost 100,000 plants. All these plants showed uniform chaff colour resembling that of the normally recessive white-chaffed parent. Darlington considers that a single dominant factor **W** in *T. polonicum* inhibits the grey chaff colour of *T. turgidum* (**ww**), and that autosyndesis in the F_1 (**WWww**) and later generations results in their breeding true.

Shift was also found by Vavilov and Jakuskhina (1925) in the cross *Triticum persicum* Vav. var. *fuliginosum* Zhuk. × *T. durum* var. *hordeiforme*. The beak-like tooth to the glume, like that of *T. durum*, was never recovered among 566 F_2 and 4,000 F_3 plants.

Another possible example of shift is the suppression and accentuation of characters, observed by Backhouse (1918) in the cross of *T. polonicum* with Kubanka.

Autosyndesis and Allosyndesis in one Organism. In the above case it will be seen that the heterozygosity of the plant is unsuspected until autosyndesis is interrupted by rare allosyndetic pairing. That allosyndesis occurs regularly between some chromosomes in some allopolyploids is shown by the behaviour of *Primula Kewensis* and of the hybrid ($2n = 28$) between *Fragaria bracteata* and *F. Helleri*, both of which have 14 chromosomes in the somatic tissue (Ichijima (1926, 1930) and Yarnell (1931)).

In both these forms the cytology indicates that autosyndesis is most prevalent but in *P. Kewensis* (hybrid of *P. floribunda* and *P. verticillata*) one quadrivalent is found at meiosis together with the expected bivalents. This quadrivalent indicates that one pair of *floribunda* chromosomes is homologous at least in part with one pair of *verticillata* chromosomes. Allosyndesis also occurs in the *Fragaria* hybrid where one quadrivalent is found together with ten bivalents. In *Primula Kewensis* no genetical segregation was found to correspond with the random pairing between the chromosomes of *floribunda* and *verticillata* (in the quadrivalent). In *Fragaria bracteata* × *F. Helleri*, however, Yarnell (1931) found that the F_1 plants were heterozygous for pink flower colour. The parent

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F. bracteata had white flowers. The F_2 plants, seven in number, were all pink-flowered. Further breeding analysis showed that the genetic constitution of these seven F_2 plants was :—

	PPPP	**PPPp**	**PPpp**	**Pppp**	**pppp**
observed	0	1	2	4	0
expected	0·19	1·55	3·5	1·55	0·19

The numbers are small but indicate that the F_1 plant was of the constitution **PPpp** and that random pairing had occurred among the two pairs of chromosomes which carried the factors respectively for pink and white flower colours from *F. Helleri* and from *F. bracteata*.

An important example showing non-segregation of factors borne on chromosomes with autosyndetic pairing, and segregation of factors borne on chromosomes which pair allosyndetically and at random, is that of the *Rubus* hybrid RT_4 ($2n = 28$).

It will be remembered that RT_4 arose from the union of an unreduced egg of *Rubus rusticanus inermis* ($2n = 14$) with a normal pollen grain of *R. thyrsiger* ($2n = 28$) (see p. 171). *R. rusticanus inermis* is a form of *R. rusticanus* without prickles. The type *R. rusticanus* however develops prickles along the angles of the furrowed stem and does not develop acicles or pricklets. *R. thyrsiger* develops prickles which are not confined to the angles of the stem. RT_4 developed its prickles directly and they were confined to the angles of the stem as in *R. rusticanus*. The selfed progeny of RT_4 consisted of prickled and unprickled plants. *All* the prickled plants behaved in the same way as RT_4 with regard to development of prickles, *i.e.*, *rusticanus* type of prickles on the mature growth. This implies that the F_1 plants of RT_4 each have one or more chromosomes represented two or more times in the complement derived from *R. rusticanus*. Further, the fact that RT_4 breeds true for this character (the *thyrsiger* type of prickles is never recovered) shows that in RT_4 these chromosomes pair autosyndetically.

The chromosomes containing the factors for the production of prickles, however, do not pair autosyndetically. The results obtained by Crane and Darlington (1932) are given below, along with the expectation on the various hypotheses. Obviously expectation based on random chromatid segregation or double reduction (see p. 181) fits most closely with the observed results, and Crane is of the opinion that this is the best explanation.

TABLE 36

(After Crane and Darlington, 1932)

	Prickled.	Unprickled.
F2.		
Observed numbers	835	37
Autosyndesis expectation (∞ : 0)	872	0
Random assortment expectation (35 : 1)	847·8	24·2
Allosyndesis expectation (15 : 1)	817·5	54·5
Random chromatid expectation (20·78 : 1)	832·0	40·0
F1 *back crossed to recessive.*		
Observed numbers	33	10
Autosyndesis expectation (∞ : 0)	43	0
Random assortment expectation (5 : 1)	35·8	7·2
Allosyndesis expectation (3 : 1)	32·3	10·7
Random chromatid expectation (3·67 : 1)	33·8	9·2

The cytology of RT_4 also shows that different types of pairing take place. At first metaphase bivalents, trivalents and quadrivalents are formed but only three or four chromosomes of the series are capable of forming trivalents and quadrivalents. Univalents often lag and divide on the equator at anaphase as a result of irregularity in the disjunction of the trivalents and quadrivalents.

The genetic behaviour of RT_4, which has been outlined above, shows that it contains two sets of *rusticanus* chromosomes. These have undoubtedly been contributed to it by an unreduced *rusticanus* gamete.

The case of an allopolyploid whose chromosome sets are all different has also to be considered. Thus in a tetraploid hybrid between two allotetraploid species, *e.g.*, cherry, or between a diploid and hexaploid species, *e.g.*, plum, the four sets of chromosomes may be designated *AB*/*CD*. Autosyndesis, allosyndesis, or even random pairing may take place. Further, the affinity of the chromosomes for one another may be such that *B* can pair with *A* or *C*, and *C* with *B* or *D*, but *A* may be unable to pair with *D*. Here *B* and *C* form a link between *A* and *D*, and if *B* and *C* pair, *A* and *D* may be left unpaired. Darlington considers that this is possibly the explanation of the occurrence of unpaired chromosomes in tetraploid cherries.

TABLE 37

Autosyndesis.	Allosyndesis.
Gametic output $SS_1 : S_1s : Ss_1 : ss_1$	$Ss : S_1s_1 : S_1s : Ss_1$ or $Ss : SS_1 : s_1s : s_1S_1$
i.e., S s 3 : 1	*i.e.*, no segregation or S s 3 : 1
Zygotic output S s 15 : 1	no segregation or S s 15 : 1
Random pairing.	Random chromatid pairing.
Gametic output $1SS_1 : \left\{\begin{matrix}1\,Ss\\1\,S_1s_1\\1\,Ss_1\\1\,S_1s\end{matrix}\right\} : 1\,ss_1$	S : s 22 : 6
i.e., S s 5 : 1	
Zygotic output S s 35 : 1	S s 20·78 : 1

It follows that in certain allopolyploids where different types of pairing may take place, the genetic results may be very difficult to analyse. In an allopolyploid where all the sets of chromosomes are of different kinds, the possibilities and complexity of types of pairing are greatly increased. It is not surprising, therefore, that interspecific polyploid hybrids normally give complex segregation. To recognise the particular type of segregation is often well-nigh impossible.

We have seen in *Fragaria*, *Rubus* and *P. Kewensis* that chromosomes may pair in different ways, and also examples of the resulting genetical segregation. Unfortunately segregation of factors in forms with both allosyndetic and autosyndetic pairing or with autosyndetic and random pairing has not yet been extensively studied.

If we have a plant of the chromosome constitution *AABB* carrying a pair of factors Ss on *AA* and a pair S_1s_1 on *BB* the segregation expected on the three types of pairing will be as shown in Table 37.

The gametic and zygotic outputs of plants of a constitution such as Ssss or SSSs may be similarly calculated by the reader. Obviously therefore the inheritance of characters in an allopolyploid may be comparatively simple, viz., sssS with autosyndesis, or highly complicated, viz., SSSs with autosyndesis and occasional allosyndesis.

WHEAT AND OATS

The four small grain crops, wheat, oats, barley and rye, have the basis chromosome number 7. Cereal barleys and rye are diploids with 14 somatic chromosomes, but wheat and oats occur as diploids, tetraploids and hexaploids. The diploid oat species *Avena brevis, A. strigosa, A. nuda brevis* and *A. Wiestii* are not of great agricultural value. The diploid wheat *Triticum monococcum* and the tetraploids *T. polonicum, T. dicoccum, T. persicum* and *T. dicoccoides* are also of very limited economic value, but there are some important agricultural varieties of the tetraploids species *T. durum* and *T. turgidum.* The species of greatest economic value are the hexaploids *T. vulgare, T. compactum, A. sativa* and *A. byzantina.* In this group, however, are also the relatively unimportant species *T. spelta, A. fatua* and *A. sterilis.*

It is evident that polyploidy has played an important part in the evolution of the wheat and oat species of economic value. The following evidence shows that they are allopolyploids. Constant autosyndesis in an allopolyploid with bivalent formation would give ordinary diploid segregation if the chromosomes were heterozygous for a pair of allelomorphic factors. It is significant therefore that in polyploid wheat and oats only bivalents are regularly formed at meiosis and genetically they generally behave like diploids giving 3 : 1 or 1 : 2 : 1 F_2 ratios and 1 : 1 back cross ratios. The frequency

TABLE 38

Factors controlling inheritance of some Characters common to Oats, Wheat and Barley

Oats.	Wheat.	Barley.
	GRAIN COLOUR.	
(1) B black b white (2) G grey g white (3) Y yellow y white (4) B_1B_2 black b_1b_2 white (B factors cumulative and independent) (5) B.G. black b.G. grey b.g. white (B epistatic to G.) (6) B_1B_2G. black b_1b_2G grey bb.g white (B factors independent and epistatic to G) (7) B.G.Y. black b.G.Y. grey b.g.Y. yellow b.g.y. white. (B epistatic to G and Y) (G ,, Y) (8) RY_1Y_2, RY_1y_2, Ry_1Y_2, Ry_1y_2 red, rY_1Y_2, rY_1y_2, ry_1Y_2 yellow, ry_1y_2 white (R epistatic to Y factors, Y factors independent)	(19) R_1 red r_1 white (20) R_2 red r_2 white (21) R_3 red r_3 white (22) R_1R_2, R_1R_3, R_2R_3 red r_1r_3, r_1r_3, r_2r_3 white (R factors cumulative and independent) (23) $R_1R_2R_3$ red $r_1r_2r_3$ white (R factors cumulative and independent) (24) P_1P_2 purple p_1p_2 white (P factors independent—in 4 *x* species—requires confirmation)	(45) B black or purple b yellow or white (46) Bl blue bl yellow (47) A.B violet-brown, Ab blue aB brown, ab yellow

Cases of duplicate factors are underlined. See literature key for references.

Oats.	Wheat.	Barley.
	GLUME COLOUR (25) **B** black **b** yellow (26) $\mathbf{Br_1}$ brown $\mathbf{br_1}$ yellow (27) $\mathbf{Br_2}$ brown $\mathbf{br_2}$ yellow (28) $\mathbf{Br_1Br_2}$ dark brown $\mathbf{br_1br_2}$ yellow (**Br** factors cumulative and independent) (29) **B.Br** black **b.Br** brown **b.br** yellow (**B** epistatic to **Br**)	(48) **B**. black **b**. white (49) **B.P.** black **b.P.** purple **bp** white (B epistatic to P) (50) $\mathbf{P_1P_2}$ dark purple $\mathbf{P_1p_2}$, $\mathbf{p_1P_2}$ light purple $\mathbf{p_1p_2}$ white
	PUBESCENCE	
Glume. (9) **P** pubescent **p** glabrous (10) $\mathbf{P_1P_2}$,, $\mathbf{p_1p_2}$,, (**P** factors independent) *Back of Grain.* (11) $\mathbf{P_1p_2}$ pubescent lower and upper grain, $\mathbf{P_1P_2}$ pubescent lower and glabrous upper grain, $\mathbf{p_1P_2}$, $\mathbf{p_1p_2}$, both grains glabrous ($\mathbf{P_1}$ and $\mathbf{p_2}$ complementary) (12) $\mathbf{P_1P_2}$ pubescent $\mathbf{p_1p_2}$ glabrous (**P** factors independent) *Base of Grain* (13) **G** glabrous **g** pubescent (14) $\mathbf{P_1P_2}$ pubescent $\mathbf{p_1p_2}$ glabrous (**P** factors independent)	*Glume.* (30) **P** pubescent **p** glabrous (31) $\mathbf{P_1}$ fully pubescent $\mathbf{P_2}$ half pubescent **p** glabrous (multiple allelomorphs) (32) $\mathbf{P_1P_2}$ pubescent $\mathbf{p_1p_2}$ glabrous	*Rachilla and Glume.* (51) **P** long unbranched pubescence **p** short unbranched pubescence.

(15) **O** open panicle **o** side panicle
(16) $\mathbf{O_1O_2}$ open panicle $\mathbf{o_1o_2}$ side panicle
(17) $\mathbf{O_1O_2O_3}$ open panicle, $\mathbf{o_1o_2o_3}$ side panicle
(**O** factors independent and cumulative)

HEAD TYPE

(33) **C** compact **c** lax
(34) **CL** compact **cL** lax **cl** sub-compact
(35) $\mathbf{Cl_1l_2}$ compact, $\mathbf{CL_1L_2}$ less compact, $\mathbf{cL_1L_2}$ lax
(**C** incompletely epistatic to $\mathbf{L_1}$ and $\mathbf{L_2}$, $\mathbf{L_1}$ and $\mathbf{L_2}$ independent and cumulative)

AWNS

(36) **L** awnless **l** awned
(37) $\mathbf{L_1}$ awnless, $\mathbf{L_2}$ half awned, **l** awned (multiple allelomorphs)
(38) $\mathbf{A_1A_2}$ awned $\mathbf{a_1a_2}$ awnless
(**A** cumulative and independent)
(39) $\mathbf{L_1L_2}$ awnless, $\mathbf{L_1l_2}$, $\mathbf{l_1L_2}$, $\mathbf{l_1l_2}$ awned

(52) **D** dense **d** lax
(53) **L** lax **l** dense

(54) **A** awned **a** awnless
(55) **L** awnless **l** hooded
(56) **H** hooded **h** awned
(57) **IhA** awnless, **iHA** hooded, **ihA** awned
(**I** = inhibitor of hoods and awns
H = hoods—epistatic to **A**
A = awned)
(58) **Hs** hooded, **HS** hoods partly suppressed, **hs** awned, **HS** awns partially suppressed
(59) **AKS** reduced hooded, **AKs** hooded, **AkS**, **aKS** awnless, **Aks**, **aKs**, **aks** awned
(**S** = inhibitor of awns epistatic to **A** or **K**, not completely dominant to **AK**)
(60) $\mathbf{C_1C_2}$ hooded, $\mathbf{c_1c_2}$ awnless, $\mathbf{C_1}$ and $\mathbf{C_2}$ complementary
(61) $\mathbf{A_1A_2A_3}$ awned $\mathbf{a_1a_2a_3}$ awnless
(**A** factors independent)
(62) $\mathbf{A_1A_2A_3A_4}$ awned $\mathbf{a_1a_2a_3a_4}$ awnless
(**A** factors independent)

Cases of duplicate factors are underlined. See literature key for references.

Oats.	Wheat.	Barley.
	HABIT	
	(40) S spring s winter (41) S_1S_2 spring s_1s_2 winter (42) Is spring iS winter	(63) S spring s winter (64) WI spring, Wi winter, wI, wi spring (I inhibitor of W)
	CHLOROPHYLL DEVELOPMENT	
(18) $G_1G_2G_3$ green $g_1g_2g_3$ lutescens (G factors independent)	(43) G_1G_2 green g_1g_2 albino (G factors independent—4*n* species) (44) $G_1G_2G_3$ green $g_1g_2g_3$ albino (G factors independent)	(65) G_1 green g_1 albino (66) G_2 ,, g_2 ,, (67) G_3 ,, g_3 ,, (68) G_4 ,, g_4 ,, (69) Gr ,, gr variegated (70) G_1 ,, g_1 light green (71) GG_1 green, gG_1 striped green, gg, albino (G epistatic to G_1) (72) Y green y light yellow (73) X_1 ,, x_1 xantha (yellow-inviable) (74) X_2 ,, x_2 xantha (yellow-inviable) (75) C_1 ,, c_1 chlorina (whitish-yellow—later green) (76) C_2 ,, c_2 super-chlorina (whitish yellow—later green) (77) V_1 ,, v_1 virescent (white—later green) (78) V_2 ,, v_2 virescent (white—later green) (79) Z_1 ,, z_1 zwerg (0–10° C. yellow, 20° C. green, but sterile) (80) Z_2 ,, z_2 zwerg (0–10° C. yellow, 20° C. green, but sterile) (81) L ,, l lutescens (green—later yellow—inviable)

Cases of duplicate factors are underlined. See literature key for references.

of duplicate and triplicate factors governing the inheritance of certain characters in the hexaploids also provides evidence that they are allopolyploids, resulting from the hybridisation of different species carrying similar factors affecting these characters. Duplicate factors may arise in a diploid by parallel gene mutations or duplication of parts of chromosomes, but the explanation that the similar factors have been brought into the hexaploid by the different diploid parental species is more feasible. The common occurrence of duplicate factors in hexaploid oats and wheat is in marked contrast to the diploids barley and rye where they are relatively rare. Demonstration of this fact is provided in Table 38, where the type of inheritance is shown for seven characters common to oats, wheat and barley. For these characters there are seven cases of duplicate or triplicate factors in oats, ten in wheat and only four in barley.

Allopolyploidy and hence duplicate and polymeric factors have provided these hexaploids with a distinct advantage physiologically over the diploid species. For example, it is desirable from the point of view of the welfare of the plant and the species, as well as from the economic point of view, that homozygous recessive lethal forms should occur very rarely. Thus a hexaploid heterozygous for three duplicate factors for chlorophyll production will only produce 1 albino in every 64 of its progeny. Further recessive lethal mutations will rarely show in a polymeric hexaploid as compared with in a diploid. (For mutation rate in the different species of *Avena* and *Triticum* see Stadler, 1929.) A typical example of this is the rare occurrence of albinos in hexaploid wheat and oats and the relatively frequent occurrence of albinos in diploid barley (see Table 38). Albinism has only been found once in hexaploid wheat (Smith and Harrington, 1929) and once in hexaploid oats (Philp, 1933) (see p. 219). In wheat it was inherited on a three-factor basis, while in oats the inheritance of more than one factor is concerned. Another example is that of a black Swedish oat having only one factor for black, which through mutation gave 10–20 white grains per kilo—an undesirable mixture. By crossing this black variety with an inferior black variety having two factors for black, another good variety with two factors for black was obtained which gave practically no white grains (Akerman, 1921*b*). If the rate of mutation in this new two factor black variety was the same as in the single factor black variety, only one white grain would appear in every 100,000,000. An undesirable feature of polymeric factors is that where recessive lethal mutations take place which are cumulative in their effect, the plant may survive and yet be adversely affected in its growth.

SPELTOIDS AND FATUOIDS

In cultivated hexaploid wheat, *Triticum vulgare Hort.* ($2n = 42$) and oats, *Avena sativa L.* ($2n = 42$) unbalanced chromosomal forms have been found as mutants. One class with a chromosome deficiency is called the B type, and another with a chromosome in excess is called the C type while a third type, A, has the normal chromosome number.

The three mutant types are morphologically identical both in wheat and oats. The wheat mutants resemble *T. Spelta L.*, and are called speltoids. The oat mutants are like *A. fatua L.*, and are called fatuoids.

The speltoids differ from the parental type in having lax ears, thick keeled glumes which can only be pulled away from the grain with difficulty, and by the presence of awns. The fatuoid oat differs from the normal parental variety in 3 main characters of the grain—articulation, pubescence and awn development. In each case the group of speltoid or fatuoid characters remain completely linked in their genetical behaviour. Generally, these mutants appear first of all in the heterozygous form, which is intermediate between the normal and the homozygous mutant. Frequently they occur as chimæras in wheat (Akerman, 1927), and one such case has been reported in oats by Huskins (1928*b*).

The genetical behaviour of speltoids is very complicated. The literature on this subject has been summarised by Kajanus (1927) and Watkins (1930). Fatuoids, on the other hand, are simpler in their genetical behaviour. The earlier literature on fatuoids has been dealt with by Stanton, Coffman and Wiebe (1926), Huskins (1927), and by Jones (1930).

Type A. Heterozygous fatuoid or speltoid mutants on selfing give in their progeny homozygous mutants, intermediate heterozygotes and normals in the ratio of approximately 1 : 2 : 1. All these classes of segregates have the normal chromosome number 42.

Winge (1924) suggested that the hexaploid *T. vulgare* had 21 chromosomes in its gametes which consisted of 3 sets of 7 chromosomes. Further, he supposed that the corresponding chromosomes in each set differed from one another only in a minor degree. Thus a chromosome *A* from one set had corresponding chromosomes *B* and *C* in the other two sets, and *A*, *B* and *C* differed from one another very slightly. (Huskins—see later—in adopting this hypothesis, attributes the slight dissimilarity between the *B* and *C* chromosomes to the hybrid origin of the hexaploid species. Winge implies that it is due to very slight differentiation of the chromosomes following direct triplication of the chromosomes of a single diploid species.) *B* is taken to be carrying the speltoid factors and *C* the normal factors which are epistatic to the speltoid factors. Considering only this group of chromosomes, normal *T. vulgare* would have the formula represented by $\frac{ABC}{ABC}$.

Owing to the close similarity between the *B* and *C* chromosomes, Winge assumed that occasionally the *B* pairs with *C* (allosyndesis) instead of normally with *B* (autosyndesis) and so gives rise to the gametes *ABB* and *ACC*. The gamete *ABB* uniting with a normal gamete *ABC* would therefore give rise to a heterozygous speltoid $\frac{ABB}{ABC}$. This heterozygote would give in the next generation, normals, heterozygous speltoids and homozygous speltoids $\frac{ABB}{ABB}$ in the ratio 1 : 2 : 1. In support of this hypothesis Winge observed a trivalent and univalent in an A type heterozygous speltoid with 42 chromosomes. These he considered were the three *B* chromosomes paired and the *C* chromosome unpaired. In a homozygous speltoid of the same strain also having 42 chromosomes he found indications of four chromosomes being associated, presumably the four *B* chromosomes.

Huskins (1927, 1928*a*,*b*) found that a characteristic feature of the cytology of the A type heterozygous fatuoids and speltoids was the formation of a trivalent while in the homozygous mutant form of the A type a quadrivalent frequently occurred. He also found that the normal segregates from a heterozygote showed greater irregularity in meiosis than the normals of a pure line. This is probably associated with the higher percentage of bad pollen produced by normal segregates as compared with a cultivated pure line. Heterozygous and homozygous fatuoids also produced more bad pollen than their normal sister plants. Huskins suggests from this evidence that the slight deficiency of the fatuoid classes which he and other workers have observed, is due to differential elimination of fatuoid gametes.

The genetical evidence obtained by Watkins and Cory (1931) of a small percentage of allosyndesis in wheat may be regarded as evidence in favour of the hypothesis that A type fatuoids and speltoids arise as a result of abnormal pairing between the *B* and *C* chromosomes.

If this hypothesis is correct, then not only does it represent a case of the breakdown of a process of constant autosyndesis (equivalent to the breakdown of a shift), but also a case of the effect of chromosomal unbalance; the heterozygote may be denoted as $6x - 1 + 1$.

The old view that fatuoids arose through natural crossing between *A. sativa* and *A. fatua* is quite untenable, since besides the occurrence of fatuoids as chimæras on normal plants, other characters such as grain colour and delayed germination have not been transmitted from *A. fatua* along with the fatuoid complex.

The chromosomal explanation of the origin of A type fatuoids and speltoids however is not universally accepted. Several workers have believed that the fatuoids differ from the normal only by a single factor difference. Nilsson-Ehle (1921*a*) is of the opinion that fatuoids arise as a result of a complex gene mutation involving a group of very closely linked factors taking place in one germ cell of the normal plant. This latter view has been widely accepted.

Jones (1930) found a mutant which was phenotypically like a heterozygous fatuoid. This intermediate fatuoid type bred true and genetically it behaved like a true fatuoid. It only differed from the normal in this particular set of characters which behaved as a single unit in inheritance. A similar type was reported by Huskins to have occurred in another variety. In the F4 of a cross, Red Algerian × Golden Rain, Jones found another type which he called " sub-fatuoid " or " semi-steriloid." Again this type behaves genetically like a true fatuoid. Jones holds the view that A type fatuoids arise through gene mutation in the *C* chromosome. The loss of the *C* chromosome in the B type heterozygotes (see later) he regards as equivalent to a loss mutation thus unmasking the fatuoid characters carried by the *B* chromosomes. He therefore considers that the different heterozygous mutants have arisen through mutations of different degrees of complexity occurring in the *C* chromosome. Huskins suggested that the true breeding intermediate fatuoid forms might have arisen by gene mutation or deficiency mutation or by crossing over between " semi-homologous" chromosomes. In connection with the latter suggestion Jones points out that if the *B* chromosome pairs with the *C* chromosome to give rise to the heterozygous A type fatuoid, it might be expected that the intermediate fatuoid type would occur in some definite percentage frequency in the progeny of an A type heterozygous fatuoid. No evidence of this has been obtained by Jones.

From a cytological study of A type fatuoids Nishiyama (1931) concludes that the meiotic irregularities need not necessarily be a result of the fatuoid constitution of the plants. Further, he obtained forty-one chromosome normal and fatuoid plants as well as forty-one chromosome heterozygous fatuoids (see p. 217). He points out, however, that of the forty-one chromosome types those having lost the *C* chromosome occurred in a higher proportion. This he states may be due to the *C* chromosome showing meiotic irregularity more often than the other chromosomes, or to a limited number of chromosomes taking part in these irregularities. There is also the possibility however that the products of the meiotic irregularities involving the *C* chromosome may be more viable than those involving other chromosomes. It appears therefore that this evidence is not in great opposition to the chromosomal aberration hypothesis.

A similar line of argument to that of Jones may be advanced against the origin of the A type speltoids on the chromosome hypothesis. In addition to the speltoid mutants there are so-called partial mutants from the beardless normal, namely, half-bearded normal, bearded normal and beardless speltoid. The characters bearded and speltoid are completely linked and crossing-over in the

A type heterozygous speltoid rarely, if ever, occurs. (Nilsson-Ehle, 1927 *et al.*). This is contrary to Winge's (1924) suggestion that the partial mutants arise through crossing-over between the *B* and *C* chromosomes. It is possible however that when *B* and *C* pair, crossing-over may not occur within the speltoid or fatuoid complexes : see Jones (1932) and Philp (1932). Perhaps very rare and particular cross-overs in other regions of these chromosomes may lead to the production of the partial mutants.

The only exception to complete linkage between the characters bearded and speltoid, apart from species crosses (Watkins, 1928), is that obtained by Nilsson-Ehle (1927), from a cross, bearded normal × beardless speltoid. In F_2 and F_3 the cross-over value between bearded and speltoid was 27%. The question therefore arises as to why the A type mutant arising through pairing of the *B* and *C* chromosomes with no crossing-over, continues to give no crossing-over in later generations, whilst the partial mutant, if produced through pairing of the *B* and *C* chromosomes with crossing-over, continues to give crossing-over in subsequent generations !

Nilsson-Ehle considers that these mutants arise through loss mutation. Owing to their linkage behaviour he regards the two factors bearded and speltoid as lying some distance apart on the chromosome. He supposes that a complex mutation takes place involving not only these two factors but also the factors lying between them, thus preventing crossing-over.

The mutant beardless speltoid, he considers, arises through mutation of the single factor bearded and therefore crossing-over is possible.

Since the cross-over percentage between bearded and speltoid is about 27% and between half-bearded and speltoid is about 36% he believes that the factor for half-bearded lies further from the speltoid factor than the bearded factor. Since no crossing-over can occur between bearded and half-bearded these factors behave genetically like multiple allelomorphs. Watkins (1930) thinks that this indicates that these two factors influence the amount of crossing-over.

Types B and C. From the hypothesis by which he attempted to explain the origin and genetical behaviour of A type speltoids Winge also postulated the occurrence of speltoids with an unbalanced chromosome number $\left(\frac{ABo}{ABC}\right)$ heterozygotes, $\left(\frac{ABo}{ABB}\right)$ and $\left(\frac{ABBB}{ABB}\right)$ homozygotes.

Huskins (1927, 1928*a,b*) found heterozygous speltoids and heterozygous fatuoids having either 41, 42 or 43 chromosomes. Those with the normal number 42 were of the A type. The 41 chromosome plants were the B type and the 43 chromosome plants were the C type. The heterozygous fatuoids with 41 chromosomes gave ratios varying from 1 : 5 to 1 : 10 normals to heterozygotes plus a few dwarf sterile homozygous fatuoids. In this respect they correspond to the B type speltoids. Similarly, the B type of heterozygous speltoid was found to have 41 chromosomes. The dwarf and sterile homozygous fatuoid segregates contained only 40 chromosomes.

In one strain of fatuoids Huskins obtained a ratio of approximately 1 : 1 normals to heterozygotes together with a few dwarf sterile homozygous fatuoids. Two heterozygotes of this, the C type, were examined; one had 43 chromosomes and the other had 41 chromosomes. C type heterozygous speltoids were also found to have 43 chromosomes. The dwarf and sterile homozygous fatuoid and homozygous speltoid segregates had 44 chromosomes. Normal segregates of both B and C types had the normal chromosome number of 42.

In explaining these results Huskins uses Winge's formula. B type heterozygotes are represented by $\frac{ABo}{ABC}$ and the 40 chromosome dwarf homozygotes resulting from them by $\frac{ABo}{ABo}$. The 43 chromosome C type heterozygotes are denoted by $\frac{ABCB}{ABC}$ and the 44 chromosome dwarf homozygous segregates by $\frac{ABCB}{ABCB}$.

The 41 chromosome B type heterozygotes characteristically formed 20 bivalents and 1 univalent at first metaphase. Very frequently the split halves of the univalent at first anaphase are not included in the daughter nuclei. This is regarded as the primary feature controlling the progeny ratios which are also influenced by selective elimination of unbalanced gametes and zygotes. Meiosis of the 40 chromosome dwarf sterile fatuoids was completely irregular.

C type heterozygous speltoids usually had the 43 chromosomes arranged as 20 bivalents and 1 trivalent. Huskins suggests that probably as a result of the method of pairing and disjunction, gametes with 21 chromosomes are formed more often than gametes with 22 chromosomes, thus affecting the ratios. The ratio is further modified by the selective elimination of unbalanced gametes and zygotes. The occurrence of a heterozygous fatuoid having 41 chromosomes in the progeny of a C type substantiates Nilsson-Ehle's statement that C types sometimes give rise to B types. The dwarf sterile homozygous fatuoids with 40 chromosomes have somewhat irregular meiosis. At first metaphase 22 bivalents, or 20 bivalents and one quadrivalent are formed, but pollen degeneration takes place at a later stage.

Håkansson (1930*b*, 1931) also observed that B and C type heterozygous speltoids had 41 and 43 chromosomes respectively, and Müntzing (1930*c*) also found a speltoid mutant having 43 chromosomes.

Among the progeny of the cross *T. vulgare* var. Marquis × *T. compactum*, Vasiljev (1929) found a heterozygous speltoid with 41 chromosomes, *i.e.*, B type. Its normal segregates had 42 chromosomes and the homozygous fatuoid segregates had 40 chromosomes. The ratios of the three classes suggests that it is also of the B type. (Philiptschenko, 1929.)

The ratio given by heterozygous fatuoids with 41 chromosomes. studied by Nishiyama (1931), was 0·1 normal : 1·5 heterozygote : 1 dwarf sterile homozygous fatuoid. This is different from Huskins' strain, which gave 1 : 5–10 : few dwarf and sterile. Possibly this is due to differences between the two races in the viability of the unbalanced gametes or to certation between the gametes with 20 and 21 chromosomes.

Nishiyama also draws attention to an interesting point concerning the balance of the *B* and *C* chromosomes or groups of factors in the formulæ used for the C types of fatuoids. In the heterozygotes of the B type the proportion of *C* to *B* is 1 : 2, which is the same as in homozygous fatuoids of the C type. This indicates that the phenotype of the C type homozygous fatuoids should approach that of a heterozygote. This may actually be the case but it has never been reported. If, on the other hand, the C type homozygous fatuoids are phenotypically true fatuoids the formulæ based on Huskins' chromosome hypothesis and Jones' mutation hypothesis, $\frac{ABCB}{ABCB}$ and $\frac{ABCC_2}{ABCC_2}$ respectively, seem less convincing.

These chromosomal mutants in oats and wheat therefore illustrate that the loss or gain of a chromosome in a polyploid has less effect on the viability of the plant as compared with a diploid. They also show the effect of chromosomal unbalance on the phenotype. This is of particular interest in this case because it permits the production of some characters typical of another species. It is also important in that it demonstrates their allopolyploid nature. Further, they show the effect of chromosomal unbalance in the type of ratios the heterozygotes produce.

The explanation on the chromosomal basis with regard to the B and C types of fatuoids and speltoids seems to be beyond dispute but there appears to be some doubt concerning the origin of the A types.

Throughout the literature on speltoids there is evidence of great variation in the ratios obtained and of the occurrence of aberrant types. Unfortunately, some workers have not allowed for the effect of winter-killing which vitiates the results. Moreover, natural crossing in these strains takes place fairly frequently as a result of their pollen sterility, especially in those plants with abnormal chromosome numbers, and many of the aberrant types may have arisen in this way. It is therefore difficult to be certain about the results which do not appear to fit in with the chromosome hypothesis. Moreover, as Huskins has pointed out, these strains are cytologically irregular—deficiency of parts of chromosomes, segmental interchange and crossing-over between the *B* and *C* chromosomes may take place, all of which add to the general complexity of the problem. In this way the genetical ratios may become modified and more complicated. In addition it is possible that the *A* chromosome may contain factors similar to those of the *C* chromosome. Philp (1935) was able to show that the inheritance of a form of albinism in oats was associated with chromosome behaviour similar to that of the *C* chromosome. Green hybrids of

A. sativa × *A. fatua* segregated in the ratio 1 green : 6 white seedlings. The green plants had 41 chromosomes, the albino plants had 40 chromosomes—the ratio depends on the amount of elimination of the extra chromosome. The extra chromosome carried a dominant green gene in the presence of which the genes for albinism did not express themselves. By crossing-over between this chromosome and a comparable chromosome of different phylo-genetic origin, plants were obtained which were either pure-breeding for green or segregated 3 green : 1 albino. Philp (1938) has demonstrated similar phenomena between broad and narrow leaved oats.

Allopolyploidy and Evolution. The evolutionary importance of allopolyploidy cannot be over-emphasised. The realisation that such forms are prevalent has changed the genetical outlook on many problems. We have already touched upon the subject of hybrid vigour, and here attention should be drawn to the phylogenetic viewpoint.

Obviously the parental species of *Primula Kewensis* had a common origin, and since differentiation one from the other, their chromosomes have undergone translocation, inversion and interchange. The same applies to the tetraploid *Fragaria* and other polyploids. Genetical material may have altered to such an extent that the chromatin parts formerly homologous are now non-homologous. The appearance in these hybrids of a quadrivalent indicates that differentiation of chromosomes has not proceeded equally among all the chromosomes. This, of course, is to be expected.

In allopolyploids of long standing there is greater probability that autosyndesis will take place since the presence of more than two homologous chromosomes will reduce fertility (see p. 176). It is, therefore, almost a constant feature of wild polyploids that they are allo- and not autopolyploids.

For similar reasons in allopolyploids as in structural hybrids, the results of any differentiation of chromosomes or of their genetic material will be less affected by natural selection than in diploids. There may therefore be difficulty in determining the original diploid progenitors of an allopolyploid of long standing.

Study of meiosis alone in an allopolyploid whose ancestry is unknown does not help very much in this direction. Under these circumstances it is difficult to determine which type of pairing is taking place. Meiosis of hybrids between an allopolyploid and other species, preferably diploid species, however, provides this evidence. For example, Ljungdahl (1924) found that the hybrid between the polyploid *Papaver striatocarpum* ($2n = 70$) and the diploid *P. nudicaule* ($2n = 14$) had 42 chromosomes which paired to form twenty-one bivalents. Clearly seven *nudicaule* chromosomes paired with seven *striatocarpum* chromosomes (allosyndesis) and the remaining twenty-eight *striatocarpum* chromosomes paired among themselves (autosyndesis). Thus it may be deduced that a diploid ancestor of *P. striatocarpum*, if not identical with *P. nudicaule*, was very closely related to it. Further, *P. striatocarpum* probably has two other diploid ancestors which were closely related and probably of common ancestry. In such hybrids pairing among all the chromosomes does not always occur ;. very often allosyndesis occurs and the rest of the chromosomes remain unpaired. *Papaver somniferum* ($2n = 22$) × *P. orientale* ($2n = 42$) gives a hybrid with 32 chromosomes. Ljungdahl (1922) found that eleven bivalents and ten univalents were formed at meiosis, and it is considered that allosyndesis had taken place between the *somniferum* and *orientale* chromosomes while the remainder of the *orientale* chromosomes remain unpaired. Again it is concluded that *P. orientale* is an allopolyploid, one of whose ancestors are closely related phylogenetically to *P. somniferum*. Similar examples to this are to be found in *Nicotiana* (see p. 305).

Genetical work may indicate the probable origin of a polyploid isolated by cytological means. Thus Lawrence (1933) has shown that *Dahlia variabilis* is most probably a hybrid between the two sections of *Dahlia* which differ in anthocyanin and flavone pigments. *Dahlia variabilis* is the only species which combines both series of genes for these pigments in one species. Likewise *Prunus domestica*, a hexaploid, combines colours of fruit of *P. cerasifera* and *P. spinosa*. Consequently Crane was of the opinion that these species or similar ones were the putative parents. Rybin has synthesised forms resembling the commercial plum by doubling the chromosomes of the hybrid *P. spinosa* × *P. divaricata* (Crane and Lawrence, 1938).

Secondary Pairing. A cytological phenomenon known as "secondary pairing" is of great assistance in determining the distant relationships between the different sets of chromosomes in allopolyploids and hence their parentage. Further, it has provided an explanation of the cause of the complexity in genetic segregation in certain cases.

Secondary pairing has only been observed in polyploids having small chromosomes, and it consists of groups of bivalents lying close together at first and at second metaphase. This is not due to chiasma formation, but is considered to be a generalised attraction analogous to that of the homologous pairs of chromosomes at metaphase in mitosis. The attraction is taken to indicate some slight degree of similarity between the chromosomes concerned. Secondary pairing was first clearly shown by Kuwada (1910), and has been observed by Ishikawa (1911), Rybin (1927), Crane and Darlington (1927), Meurman (1929), Lawrence (1929, 1931*a*,*b*,*c*), Darlington and Moffett (1930), and Moffett (1931). It is discussed in detail by Darlington (1931*a*) and Lawrence (1931*c*). Caution in accepting the implications of secondary pairing is necessary in the light of our knowledge of structural changes.

In RT_4 and in the parent tetraploid species *Rubus thyrsiger* secondary pairing occurs (Crane and Darlington, 1927). This shows that there is some similarity between the chromosome sets of *R. thyrsiger*, and hence confirms the genetical evidence of autosyndesis in RT_4.

Secondary Polyploids. Cytological studies of the *Pomoideæ* by Darlington and Moffett (1930) and Moffett (1931) where multiple association of chromosomes and secondary pairing were observed are of great importance, especially with regard to their conclusions.

The basic chromosome number of *Pyrus* is 17. Diploid varieties of apples with 34 somatic chromosomes and triploid varieties with 51 somatic chromosomes occur in cultivation. In meiosis of diploids Darlington and Moffett found that seventeen bivalents were usually formed and that secondary pairing also occurred. The degree of secondary pairing was variable. Generally nine bivalents formed three groups of three, and eight bivalents formed four groups of four. In isolated cases this form of grouping was found complete in a cell, *i.e.*, seven groups of chromosomes when seventeen would be expected if no secondary pairing had taken place. Trivalents were usually formed in triploids, but associations of from four to nine chromosomes occurred, the association of nine chromosomes, however, being rare.

They conclude that secondary pairing in the diploids is evidence of similarity of certain chromosomes within the sets, but the degree of similarity is insufficient to allow of autosyndesis. Multiple associations of chromosomes in the triploids confirm this view. They consider that the third set of chromosomes make a bridge between the secondarily associated bivalents of the diploid, indicating that autosyndesis occurs within each of the supposed three haploid sets. They therefore conclude that the diploid has really only seven types of chromosomes; three are represented six times and four are represented four times, *i.e.*, it is a trebly hexasomic tetraploid. The haploid chromosome complement of the diploid apple may be represented thus :—

AAA
BBB
CCC
DD
EE
FF
GG

The derived series of polyploids in the Pomoideæ ($2n = 34, 51, 68$) they regard as secondary polyploids having a primary basic chromosome number of seven, the number seventeen being a secondary basic number.

In support of these conclusions they quote the following evidence, Among natural seedlings of the triploid apple variety, Bramley's Seedling ($2n = 51$) (almost certainly their male parents were diploid varieties) those having 41 chromosomes were most frequent. From a normal triploid with 51 chromosomes it would be expected that those plants having 25 or 26 + 17, *i.e.*, 42 or 43 chromosomes, would be most frequent among the progeny. The number 41, however, happens to be the sum of the primary haploid number 7 and the secondary diploid number 34. Thus they suggest that the 41 chromosome seedlings predominate because of their chromosome balance; they have obtained the primary balance of 7 and the secondary balance of 17.

Further support of this hypothesis is provided by the fact that certain types of somatic chromosomes can be recognised to be represented in the expected number of times. Moffett (1931) has made a cytological study of a large number of the *Pomoideæ*, and found that they all agree with the conclusions arrived at from the study of the apples.

Darlington and Moffett point out that *Rosa, Rubus, Geum, Fragaria* and *Potentilla* have the basic number seven, and they suggest that the production of this secondary basic number has been a definite evolutionary step towards producing the *Pomoideæ*.

It is not surprising that the cytological complexity of the apple should be reflected in its genetic behaviour. This is shown to be the case with regard to its behaviour concerning incompatibility. Table 7 shows that fewer varieties of apples are self-incompatible than in either hexaploid plums or diploid cherries. It also shows that the frequency of both self and cross incompatibility in apples, plums and cherries increases as the cytological complexity decreases. Reference to the method of inheritance of incompatibility in diploids will illustrate why this result is to be expected (see p. 40).

The general genetic behaviour of diploid and hexaploid *Prunus* species and the apple may be compared in order to demonstrate the correlation between degree of cytological complexity and degree of genetical complexity. In diploid plums, cherries and peaches, variation in most of the characters so far studied is discontinuous and distinct (Crane, 1921).

In hexaploid plums, variation is much less discontinuous and less distinct than in diploid species of *Prunus*. In apples, inheritance is more complex than in hexaploid plums (Crane and Lawrence, 1933). A few characters are discontinuous, but many show almost complete intergradation from one extreme to the other.

Conclusions. The outstanding feature of allopolyploids is that their genetic behaviour depends on the type of chromosome pairing at meiosis, which may be autosyndetic, allosyndetic, or free pairing. Pairing in turn depends on the relationships of the chromosomes, and hence on the ancestry of the allopolyploid. Variation in the degree of relationship of the chromosomes in an allopolyploid results in much variation in type of pairing, and hence to very complex genetic segregation.

CHAPTER VIII

EUPLOIDS AND ANEUPLOIDS

Triploids—Primary, secondary and tertiary trisomics—Trisomic Inheritance —Balance—Haploids.

TRIPLOIDS

Origin. Triploids may be produced experimentally by intercrossing diploids and tetraploids. They occur in nature through the mating of gametes containing $2x$ and x chromosomes respectively. Thus, triploids have been found among normal diploid plants in tomato (Lesley and Mann (1925), Lesley (1928)), *Tulipa* (Newton (1926), Newton and Darlington (1929), de Mol (1928, 1929)), *Hyacinthus* (de Mol (1927*a,b*), Darlington (1929*b*)), *Aconitum* wild species (Darlington, unpublished), *Narcissus* (Nagao, 1929), *Pomoideæ* (Darlington and Moffett (1930), Moffett (1931)), and in many other genera. These have arisen presumably from a diploid plant through the production of a gamete with the unreduced number of chromosomes. The morphology of triploids, like tetraploids, is usually similar to that of the related diploid, but the habit is more vigorous. Earlier workers emphasised this difference by designating the triploid and tetraploid forms of a species with the names *semi-gigas* and *gigas* respectively. There are a few examples, such as *Raphanus-Brassica, Primula Kewensis* and *Rubus,* where the triploid shows qualitative differences from the diploid and tetraploid form. These differences arise from the interaction of factors of dissimilar phylogeny.

It is useful for the purposes of genetic discussion to make a distinction between triploids which have arisen by crossing two plants of different phylogeny and those which have arisen through the crossing of plants of similar origin. The first class of triploids, having three sets of chromosomes, of which at least one is distinct from the other two, may be called allotriploids. The second class with all three sets of chromosomes homologous may be called autotriploids.

Usually the cross $4x \times 2x$ is more productive than the reciprocal cross $2x \times 4x$. For example, the diploid forms of *Primula sinensis*, *Datura Stramonium*, *Solanum Lycopersicum*, and *Campanula persicifolia*, when used as females in crosses with the tetraploid forms, set no seed. On the other hand, the crosses *Nicotiana glutinosa* ($2n = 24$) × *N. Tabacum purpurea* ($2n = 48$), *Rubus rusticanus inermis* ($2n = 14$) × *R. thyrsiger* ($2n = 28$) and *Phleum pratense* ($2n = 14$) × *P. alpinum* ($2n = 28$) are fertile and produce triploids.

The reciprocal cross $4x \times 2x$ has given rise to most of the experimentally produced triploids, *Primula sinensis* (Sömme (1930), de Winton and Haldane (1931)), *Datura* (Blakeslee, Belling and Farnham, 1923), *Solanum Lycopersicum* (Lesley (1928), Sansome (unpub.)), *Campanula persicifolia* (Gairdner, 1926) and *Primula malacoides* (Philp, unpub.).

The fertility of the cross, $4x \times x$, is from 0·5% to 20% of the normal cross, $2x \times 2x$ (*cf.* Lesley and Lesley (1930), McClintock and Hill (1931), Sömme (1930), Buchholz and Blakeslee (1929)).

There are probably two main causes underlying the greater sterility of the cross, $2x \times 4x$, as compared with the reciprocal. In *Datura* the pollen tubes carrying $2x$ chromosomes burst soon after pollination of a $2x$ style (Buchholz and Blakeslee, 1929). In *Primula sinensis* $2x$ pollen grains show greatly reduced germination (about 2%). Those which do germinate have no directional properties, as in incompatible pollinations in Gramineæ and *Tulipa* (Sansome, unpub.).

The other cause of sterility in this cross is the reaction of the $2x$ tissue of the mother plant with the $4x$ tissue of the endosperm and $3x$ embryo. The normal balance in a hybrid, diploid × diploid is, of course, mother plant tissue $2x$, endosperm $3x$ and embryo $2x$ (*cf.* Watkins (1932) and review by Müntzing (1933)).

It is noteworthy that the majority of successful crosses of the nature $2x \times 4x$, have been between species. This might be expected for the following reason. If we designate the chromosomes of one species, used as the female, as $2x$, and of the other, used as male, as $4x^1$, then the mother plant tissue is $2x$, the hybrid endosperm is $2x + 2x^1$ and the hybrid embryo is $x + 2x^1$. This is more similar to the normal chromosomal ratio of mother, endosperm and embryo,

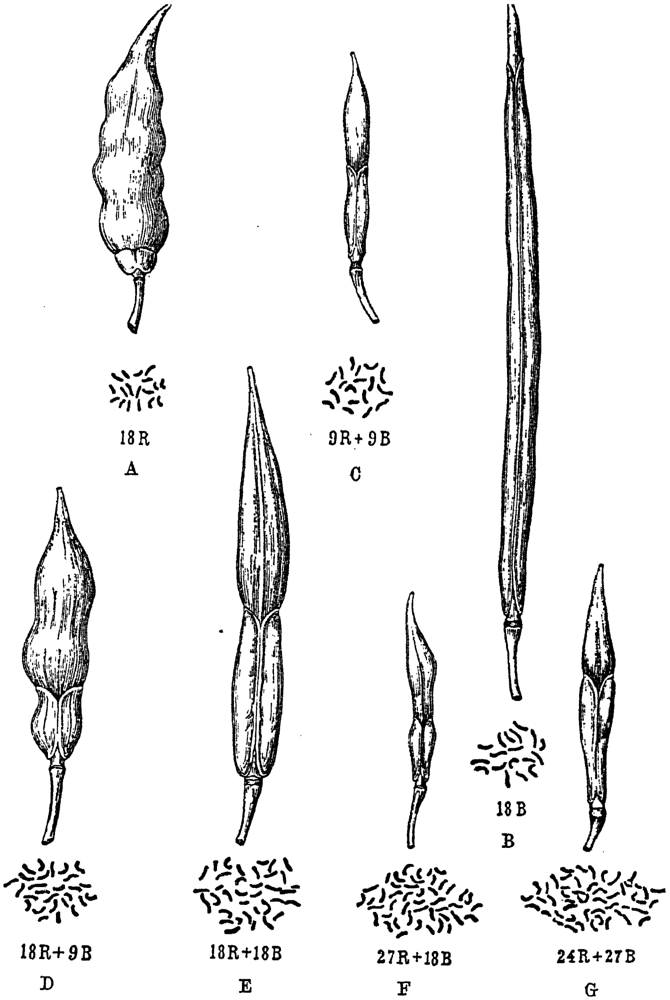


Fig. 31. Pods, somatic plates of chromosomes and formulæ for *Raphanus* (A), *Brassica* (B), diploid (C), triploid (D), tetraploid (E), pentaploid (F), and hypohexaploid (G) hybrids.
(Karpechenko, 1928.)

than in the reciprocal and more fertile cross where the ratio is: —mother, $4x$: endosperm, $4x^1 + x$; embryo, $2x^1 + x$. Müntzing

(1933) reviews the work of Watkins, Kihara, Nishiyama and Thompson on reciprocal crosses.

When the triploid results from the hybridisation of plants with differing characters, the expression of these characters is sometimes of interest. For example, *P. Kewensis* ($4x = 36$), backcrossed to one of its parents *P. floribunda* ($2x = 18$) gave two plants approximately tetraploid and three plants approximately triploid. All five plants had the thick covering of hair characteristic of *P. floribunda* which is not present in *P. Kewensis*. It is suggested that *P. floribunda* has contributed one set of chromosomes to form the triploids and two sets to form the tetraploids. Therefore in the triploids there would be two sets of *floribunda* to one of *verticillata*, and in the tetraploids three sets of *floribunda* to one of *verticillata* (Newton and Pellew, 1929).

Figure 31 from Karpechenko (1928) illustrates the remarkable behaviour of the hybrids of *Raphanus* and *Brassica*. The sterile F_1 hybrid contains nine chromosomes of *Raphanus* (R) and nine of *Brassica* (B) (see p. 168). According to the different ratios of the R : B chromosomes in derivatives, Karpechenko (1927, 1928) observed proportional variation in the characteristic shape of the siliqua of the two genera.

Similar striking examples may be found in *Rubus rusticanus inermis* × *R. thyrsiger* (Crane and Darlington, 1927), and in *Funaria hygrometrica* (Wettstein, 1924*a*).

Cytology. Cytological examination of triploids of numerous species confirms the general conclusions from genetical data and breeding work (see literature key). It has been found that trivalents are formed more frequently by the longer than by the shorter chromosomes of *Tulipa* (Newton and Darlington (1927), Darlington and Mather (1932)), *Zea Mays* (McClintock and Hill, 1931), *Hyacinthus* (Belling (1927*a*, 1929), Darlington (1929*b*), Stone and Mather (1932)). If metaphase pairing depends on the retention of chiasmata formed at prophase in meiosis, the minimum number of chiasmata required to form a trivalent is two compared with one chiasma required for bivalent formation. It is usual to find that the chiasma frequency *per* nucleus is higher in the triploid than in the comparable diploid (*Tulipa*, *Hyacinthus*, *Hemerocallis*, *Lycopersicum*). Thus the frequency of chiasma formation is not proportional to the chromosome length paired. In both diploids and triploids the length for potential chiasma formation is the length of the chromosome, but two chromosomes are available in the diploid and three in the triploid. This fact is in accordance with the varied genetical results from *Drosophila, Zea* and *Lycopersicum,* in which the crossing-over per chromosome in triploids corresponds with that in diploids.

The formation of trivalents leads to regular numerical non-disjunction of one of the three homologous chromosomes. Random distribution will therefore be represented by a binomial curve ranging from the $1x$-$2x$ number of chromosomes. Thus in 1,000 p.m.cs., of triploid *Datura* with $x = 12$, the expected and observed percentages were (Satina and Blakeslee, 1937) :—

Chromosome Assortment to the Poles at Metaphase I.

	12 + 24	13 + 23	14 + 22	15 + 21	16 + 20	17 + 19	18 + 18
Observed .	0·8%	4·5%	8·5%	14·5%	22·9%	30·8%	18·0%
Expected .	0·05%	0·6%	3·2%	10·7%	24·2%	38·7%	22·6%

It will be observed that the greatest number of p.m.cs. gave 17–19 chromosomes to each pole. The observed proportion at $1x$ and $2x$ is significantly greater than the calculated frequency (16 times more frequent). The reason for this preferential disjunction is unknown. Sturtevant (1936) and Lesley (1937) mention possible signs of non-random disjunction in *Drosophila* and *Lycopersicum.* When a trivalent is not formed but is replaced by a bivalent and univalent as a result of a low chiasma frequency or of reduction in homology as in structural hybrids or allotriploids, the irregularities of the division are greater. This is due to the fact that the univalents formed may not be included in the division spindles at the first or second meiotic divisions, and therefore are lost in the cytoplasm. When the univalent is included in the division it will divide once at either the first or second division and be distributed, possibly at random, during the alternative division. Where the divisions are very irregular, gametes may be produced with chromosome numbers higher than $2x$ as a result of random inclusion of extra univalents in a cell. (*e.g. Phleum.*) Triploids, pentaploids and haploids, therefore, are expected to give rise to progeny with unusual chromosome numbers.

In the diploid *Raphanus-Brassica* hybrid (Karpechenko, 1927*a*,*b*, 1928), where no pairing takes place between the 9R and 9B chromosomes, only gametes with approximately the diploid or tetraploid number were fertile. The selfed progeny consisted of tetraploids, a few with 37–38 chromosomes, and some plants with reduced development and other peculiarities had about 54 chromosomes. No triploids were found. Triploid hybrids (18R + 9B) when selfed, gave mainly diploids, triploids and a few hyperdiploids and hypotriploids. No hypodiploids, triploids or hypertriploids were obtained.

The *Œnothera* triploid *semi-gigas* ($3x = 21$) when crossed with diploids such as *O. Lamarckiana* or *O. velutina* gave rise to progeny with chromosome numbers ranging from 14 to 20 with the mode in the 15 chromosome class (de Vries and Boedijn (1924), van Overeem (1920)).

With the exception of some *Œnothera* species, however, derivatives with the $2x$ and $4x$ chromosome numbers are most frequent, together with a few forms with chromosome numbers of the $2x+1$, $2x+2$, $4x-2$, $4x-1$, $4x+1$ and $4x+2$ types. Considerable information is provided by Satina and Blakeslee (1937*a*,*b*) who have studied the proportion of nuclei with different chromosome numbers at each stage of gametogenesis. Following the preferential production of $1x$ and $2x$ nuclei at Division I mentioned above there is an elimination of lagging chromosomes at Division I and II, gametic abortion, and preferential functioning on both male and female sides. These increase the proportion of functional male $1x$ gametes to as much as 3,000 times that expected on random assortment and the female $1x$ gametes to a less extent!

Progeny of Triploids. When the cross $3x \times 2x$ is made in *Datura* the progeny consists of 53% of $2x + 1$ forms, 28% of $2x$ forms, 16% of $2x + 1 + 1$ forms and 1·4% of forms with other chromosome numbers. Similar proportions have been found in tomato (Lesley, 1928) and maize (McClintock and Hill, 1931).

Selfing a triploid *Datura* generally gives a small proportion of tetraploids together with 56% of $2x + 1$ forms. The proportion of tetraploids from selfed triploids of tomato is much higher than in

Datura. Unfortunately, there are little data of the cross $3x \times 2x$ in *P. sinensis* or tomato.

The reason for the discrepancy between the observed chromosome numbers of triploid derivatives and those expected from cytological examination is bound up with the viability of the gametes and zygotes. This in turn depends on the genetical constitution. It is expected that the behaviour of factors in a normal haploid nucleus will be different from that in a nucleus containing reduplicated parts of the chromatin as in $x + 1$, $x + 2$, etc., gametes. The amount of reduplication of a part of the chromatin as compared with the rest of the chromatin is probably a measure of the unbalance of the genetical constitution. Under different conditions—diploid style or embryo-sac, triploid and tetraploid style, etc.—the male gametes with different proportions of reduplications will react differently (*cf.* Darlington (1929*b*) and Darlington and Moffett (1930), etc.). This will be further considered later.

The characteristic sterility of triploids is due to the production of a large proportion of gametes containing duplications and deficiencies.

TRISOMICS

The unbalanced forms with $2x + 1$ chromosomes found in the progeny of triploids may also arise from diploids through non-disjunction of one bivalent, *e.g.*, *Matthiola incana* var. Snowflake (Frost and Mann, 1924) and *Datura.* Cold treated plants of *Datura* gave the trisomic form Poinsettia (Blakeslee and Farnham, 1923), while a whole series of forms was obtained in the progeny of a haploid *Datura* plant through irregularities in meiosis (Blakeslee, Morrison and Avery (1927), Satina, Blakeslee and Harvey (1937)).

Primary Trisomics. Together with the normal diploid complement there is an extra chromosome of the haploid set in primary trisomics. Thus in a $2x + 1$ form of maize with 21 chromosomes, it was found that 9 of the chromosomes of the basic set were represented twice, but the tenth and smallest chromosome (which carries the **r.g.** linkage group) was represented three times.

If the haploid number of chromosomes is 12 as in *Datura* and tomato, there are twelve possible types of primary trisomics corresponding to each of the twelve chromosomes. The presence of a chromosome in excess of the normal complement is accompanied by a change, which may be observable in the expression of the characters of the individual.

Blakeslee and Belling (1924*b*) and Blakeslee (1930) were able to identify all of the twelve possible trisomics of *Datura* by the shape of the fruit. Other parts of the plant were also affected, but fruit shape was more easily described and analysed. These trisomics have been named globe, poinsettia, cocklebur, ilex, echinus, rolled, buckling, glossy, microcarpic, elongate, reduced, and spinach, respectively (see Fig. 32).

Lesley (1928) identified nine out of the possible twelve trisomics of tomato, while all of the ten chromosomes of maize have been associated with known genetical linkage groups by means of the analysis of trisomics.

Trisomic Inheritance. In a plant with three homologous chromosomes *A*, *B* and *C*, random pairing followed by disjunction of two chromosomes to opposite poles and non-disjunction of the third will give the gametes *AB*, *AC*, *BC*, *A*, *B* and *C*. Therefore in a trisomic plant there will be normal disomic ratios for all factors not contained in the trivalent and a trisomic ratio for the factors borne by the trivalent.

In the light of our knowledge of chromatid segregation (the production of equational exceptions, see p. 99). it is now apparent that the segregation of each gene is influenced by the amount of crossing-over between the centromere and the locus of the gene. We may, however, obtain a first approximation by assuming chromosome segregation.

If the trisomic plant is simplex for a factor **X** (**Xxx**), the gametic output will be 1**X** : 2**Xx** : 2**x** : 1**xx** and the ratio of gametes containing the dominant and recessives will be 1 : 1.

In a duplex trisomic (**XXx**) the gametic output will be 1**XX** : 2**X** : 2**Xx** : 1**x** and the ratio of dominant to recessive gametes will be 5 : 1. Equal numbers of x and $x + 1$ gametes are expected to be formed on this assumption. It has been found, however, that the transmission of the $x + 1$ gametes is reduced in trisomics of maize, *Datura* and tomato, especially on the male side.

The degree of transmission of $x + 1$ gametes varies with the particular chromosome in excess. Thus the extra chromosome of

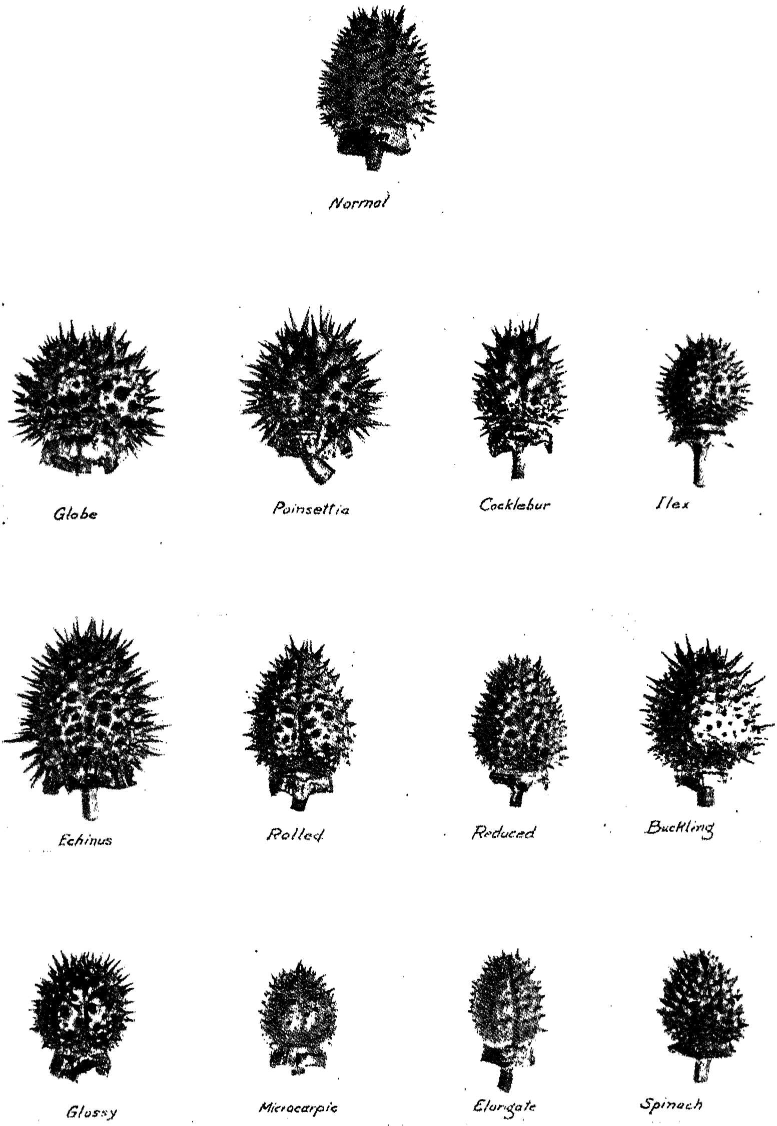


FIG. 32. Capsules of the 12 primary ($2x + 1$) types of *Datura Stramonium* with a capsule of a normal plant above.
(Blakeslee, 1930.)

the Poinsettia trisomic *Datura* is rarely transmitted through the pollen, while the Globe trisomic is transmitted in about 2% of cases. In maize and tomato the extra chromosome is rarely transmitted through the pollen.

Interesting work in this connection has been done by Buchholz and Blakeslee (1922, 1927*a,b,c*, 1929, 1930*a,b*). They were able to dissect the styles, and by suitable staining to observe the pollen tubes. They analysed all the possible crosses between the polyploid forms of *Datura* and also trisomic hybrids. They find, for example, that in the trisomic Cocklebur, the amount of pollen tube growth, twelve hours after pollination, exhibited a bimodal curve. The two modal classes corresponded to the pollen tubes carrying x and $x + 1$. The x carrying pollen grains constitute the group with greatest tube growth. The comparative rate of growth per hour was 2·6 : 1·9 mm.

The application of much pollen to the stigma reduces the proportion of $x + 1$ pollen tubes which reach the ovules. When more than 500 pollen grains from the Globe trisomic were applied to the stigma of a diploid the progeny had few trisomic plants. When the style was cut off after the fast-growing tubes had entered the ovary, only the x carrying pollen tubes were found to have functioned. Limited pollination followed by separation of the seeds from the lower and upper half of the ovary also showed that the $x + 1$ carrying tubes grew more slowly. In the upper half of the ovary only $2x$ seeds were found, while a higher proportion of $2x+1$ embryos than usual were found in the lower half (*cf.* p. 37). Pollination by a special method whereby the style was artificially shortened increased by 15 times the proportion of $(2x + 1)$ seed (Buchholz, Doak and Blakeslee, 1932).

On the female side it is found that in place of 50%, only 30% of the egg cells contain $x + 1$ chromosomes. McClintock and Hill point out that the univalent may or may not be included in the first and second divisions when a bivalent and univalent are formed instead of a trivalent (they have observed this fact). The univalent may undergo division either at the first or second division. If it is lost in the cytoplasm through not being included on the spindle, the number of x gametes will be increased at the expense of the $x + 1$ gametes (see also Satina and Blakeslee, 1937).

In *Datura* the extra chromosome is transmitted through the female side in different proportions in the different trisomics (see Table 39). The transmission of the $x + 1$ gametes through the female is greater in *Datura*, tomato and *Matthiola* when the trisomic is pollinated with a diploid or another trisomic. Blakeslee has suggested that the increased vigour of the embryo resulting from outcrossing is the reason for this.

TABLE 39

Transmission of the extra Chromosome through the Egg of Primary Trisomic Plants of Datura *and Tomato.*

Datura Stramonium		Tomato	
Globe . .	29·0%	Triplo-A . .	23%
Poinsettia. .	27·7%	„ B . .	27%
Cocklebur . .	26·39%	„ C . .	15%
Ilex . . .	32·0%		
Echinus . .	30·9%		
Rolled . .	20·1%		
Reduced . .	18·69%		
Buckling . .	30·9%		
Elongate . .	10·8%		

Table 40 gives the phenotypic ratios and genetic types to be expected from a trisomic plant on the assumption that $x + 1$ pollen tubes are non-functional.

The experimental results from *Datura* are in general agreement with the expected ratios. Those of *Lycopersicum* (Table 42) and of *Zea* (see p. 99) show disagreement as a result of the production of equational exceptions. In *Lycopersicum* the ratio of the diploid progeny apparently approaches the expected ratio, but the presence of 17d, 17p and 6s in the trisomic progeny where none is expected indicates how such qualitative evidence is much more informative than the quantitative (from the diploid progeny).

Trisomic inheritance of doubleness in *Matthiola incana*, which, however, is complicated by lethals, is given by Frost (1931).

Secondary and Tertiary Trisomics. Early in the investigations on *Datura* it was found that primary trisomics, such as Cocklebur trisomic for chromosome 11·12, gave rise occasionally to other (secondary) trisomics with different morphological features, *e.g.*

TABLE 40

Trisomic Inheritance of an Allelomorphic Pair **A**, **a** *in a* (*2n* + 1) *Mutant when the Extra Chromosome is not carried by the Pollen. Formulæ for Parents, Gametes and both 2n and* (*2n* + 1) *Offspring* (*Blakeslee and Farnham,* 1923).

Female Parent (gametes in parenthesis).	Pollinated by	2n Offspring.				(2n + 1) Offspring.				
		A_2	Aa.	a_2.	Ratio A : a	Ratio A : a	A_3	A_2a	Aa_2	a_3.
A_3 (A_2+A)	A_3	1	.....	.....	1 : 0	1 : 0	1	.....	.....	.....
	A_2a	2	1	.....	1 : 0	1 : 0	2	1	.....	.....
	Aa_2	1	2	.....	1 : 0	1 : 0	1	2	.....	.....
	a_3	.....	1	.....	1 : 0	1 : 0	.....	1	.....	.....
	A_2	1	.....	.....	1 : 0	1 : 0	1	.....	.....	.....
	Aa	1	1	.....	1 : 0	1 : 0	1	1	.....	.....
	a_2	.....	1	.....	1 : 0	1 : 0	.....	1	.....	.....
A_2a (2A+a+A_2+2Aa)	A_3	2	1	.....	1 : 0	1 : 0	1	2	.....	.....
	A_2a	4	4	1	8 : 1	9 : 0	2	5	2	.....
	Aa_2	2	5	2	7 : 2	9 : 0	1	4	4	.....
	a_3	.....	2	1	2 : 1	3 : 0	.....	1	2	.....
	A_2	2	1	.....	1 : 0	1 : 0	1	2	.....	.....
	Aa	2	3	1	5 : 1	6 : 0	1	3	2	.....
	a_2	.....	2	1	2 : 1	3 : 0	.....	1	2	.....
Aa_2 (A+2a+2Aa+a_2)	A_3	1	2	.....	1 : 0	1 : 0	.....	2	1	.....
	A_2a	2	5	2	7 : 2	8 : 1	.....	4	4	1
	Aa_2	1	4	4	5 : 4	7 : 2	.....	2	5	2
	a_3	.....	1	2	1 : 2	2 : 1	.....	.....	2	1
	A_2	1	2	.....	1 : 0	1 : 0	.....	2	1	.....
	Aa	1	3	2	4 : 2	5 : 1	.....	2	3	1
	a_2	.....	1	2	1 : 2	2 : 1	.....	.....	2	1
a_3 (a+a_2)	A_3	.....	1	.....	1 : 0	1 : 0	.....	.....	1	.....
	A_2a	.....	2	1	2 : 1	2 : 1	.....	.....	2	1
	Aa_2	.....	1	2	1 : 2	1 : 2	.....	.....	1	2
	a_3	.....	.....	1	0 : 1	0 : 1	.....	.....	.....	1
	A_2	.....	1	.....	1 : 0	1 : 0	.....	.....	1	.....
	Aa	.....	1	1	1 : 1	1 : 1	.....	.....	1	1
	a_2	.....	.....	1	0 : 1	0 : 1	.....	.....	.....	1
A_2 (A)	A_3	1	.....	.....	1 : 0		.....	.....	.....	.....
	A_2a	2	1	.....	1 : 0		.....	.....	.....	.....
	Aa_2	1	2	.....	1 : 0		.....	.....	.....	.....
	a_3	.....	1	.....	1 : 0		.....	.....	.....	.....
Aa (A+a)	A_3	1	1	.....	1 : 0		.....	.....	.....	.....
	A_2a	2	3	1	5 : 1		.....	.....	.....	.....
	Aa_2	1	3	2	4 : 2		.....	.....	.....	.....
	a_3	.....	1	1	1 : 1		.....	.....	.....	.....
a_2 (a)	A_3	.....	1	.....	1 : 0		.....	.....	.....	.....
	A_2a	.....	2	1	2 : 1		.....	.....	.....	.....
	Aa_2	.....	1	2	1 : 2		.....	.....	.....	.....
	a_3	.....	.....	1	0 : 1		.....	.....	.....	.....

TABLE 41

Trisomic Inheritance of the Allelomorphic Characters Purple (P) *and White* (p) *flower colour in the Trisomic* Datura *Mutant Poinsettia.* (*After Blakeslee and Farnham,* 1923.)

Cross.	Number of families.	Normals.			Poinsettias.		
		P	p	$\frac{\text{Dev.}}{\text{P.E.}}$	P	p	$\frac{\text{Dev.}}{\text{P.E.}}$
$P_3 \times P_3$	10	882	0	—	263	0	—
Calculated	—	882	0	—	263	0	—
$P_2p \times P_2p$	29	1826	220	—	692	0	—
Calculated	—	1818·7	227·3±9·58	0·8	692	0	—
$\times Pp_2$	7	292	95	—	135	0	—
Calculated	—	301	86±5·51	1·6	135	0	—
$\times p_3$	2	70	46	—	49	1	—
Calculated	—	77·3	38·7±3·42	2·1	50	0	—
$\times Pp$	4	218	36	—	121	0	—
Calculated	—	211·8	42·2±4·01	1·5	121	0	—
$\times p_2$	14	645	281	—	409	0	—
Calculated	—	617·3	308·7±9·66	2·9	409	0	
$Pp_2 \times P_2p$	13	574	160	—	337	39	—
Calculated	—	570·9	163·1±7·59	0·4	334·2	41·8±4·11	0·7
$\times Pp_2$	35	1287	995	—	870	223	—
Calculated	—	1267·8	1014·2±16·01	1·2	850·1	242·9±9·27	2·1
$\times p_3$	4	171	292	—	142	75	—
Calculated	—	154·7	309·3±6·84	2·5	144·7	72·3±4·68	0·6
Pp	7	356	196	—	218	40	—
Calculated	—	368	184±7·46	1·6	215	43±4·04	0·7
$\times p_2$	10	219	436	—	206	84	1
Calculated	—	218·3	436·7±8·13	0·1	193·3	96·7±5·41	2·3
$p_3 \times P_2p$	2	412	233	—	185	109	—
Calculated	—	430	215±8·07	2·2	196	98±5·45	2·0
$\times Pp_2$	3	222	436	—	88	201	—
Calculated	—	219·3	438·7±8·15	0·3	96·3	192·7±5·40	1·5
$\times p_3$	1	0	143	—	0	73	—
Calculated	—	0	143	—	0	73	—
$\times Pp$	6	170	175	—	66	95	—
Calculated	—	172·5	172·5±6·27	0·4	80·5	80·5±4·28	3·4
$p_2 \times P_2p$	9	1958	1040	—	—	—	—
Calculated	—	1998·7	999·3±17·39	2·3	—	—	—
$\times Pp_2$	12	1166	2392	—	—	—	—
Calculated	—	1186	2732±18·94	1·1	—	—	—

Wedge (11·11). Philp and Huskins (1931), Huskins and Hunter (1933) report secondary trisomics in *Matthiola*, and Rhoades (1938) found a secondary trisomic in *Zea*.

The cytology of the secondary trisomic (Belling (1927*a*, 1928*a*), Belling and Blakeslee (1924*b*)) shows that there may be a closed ring of three chromosomes, while in a primary only a chain is possible. The hypothesis of these authors is that the secondary trisomic has three chromosomes, two of which are normal in structure and homologous, but the third has two similar ends, which are homologous with one end of one of the other two chromosomes (*cf.* diagram, Fig. 33).

The genetical behaviour of primary and secondary trisomics is different, and enables one to separate the two types. The primary trisomic gives rise to forms like itself, to normals, and to a small and irregular percentage of the related secondaries. A secondary trisomic gives rise to normals, to the related primary trisomic, and to forms like itself in definite proportions.

TABLE 42

Trisomic Inheritance of the Characters dwarf d, *peach* p, *compound* s *in the Trisomic Tomato Mutant Triplo A. (After Lesley,* 1937.)

$d_1PS/D_1ps/D_1Ps \times d_1ps/d_1ps$

	Diploid progeny.	Triploid progeny
dPS	112	6
DpS	150	17
DPs	62	5
DPS	47	191
dpS	4	0
dPs	15	1
Dps	18	0

Diploid progeny.

D/d	P/p	S/s
277/131	236/172	314/95

expected on 2 : 1 basis. 272 : 136.

Triploid progeny.

D/d	P/p	S/s
218/17	218/17	229/6

expected ∞ : 0.

TABLE 43

List of Primaries, Secondaries, and Tertiaries in Datura Stramonium *arranged by size of Chromosomes in the Trisomic set.* (*Blakeslee*, 1930.)

[Ends of chromosomes are designated by numbers 1 to 24]

1 Chromosome size class.	2 Secondary chromosomes and $(2n+2/2)$ type.	3 Primary chromosomes and $(2n+1)$ type	4 Secondary chromosomes and $(2n+2/2)$ type.	5 Tertiary chromosomes and $(2n+1)$ type.	6 Genes located in particular chromosome.
L	Py (1·1)	Rl (1·2)	Sg (2·2)	DS=2·17 Wy=1·18. ES=2·9. Ph=2·5. Hg=1·9. trSg=12·11·2	p in Wy.
l	Sm (3·3)	Gs (3·4)		Mp=4·6 (3.21). (4·22).	fw, Bz in 4 half. QS in Gs, half not yet determined.
l	St (5·5)	Bk (5.6)	At (6.6)	Mp=4·6 Ph = 2·5.	
M	Un (7·7)	El (7·8)			
M°	Mt (9.9)	Ec (9·10°)	Th (10°·10°)	SE=9·20° (10·19). ES = 2·9. Hg=1·9.	MS in either Ec or Sp.
M°	Wd (11.11)	Ck (11.12°)		trSg=12·11·2 (11·21). (12·22).	in, tf, e, sky, in 12 half.
M	Not named (13·13).	Mc (13·14)	Not named (14.14).	X=18·13	al.
M	Sc (15·15)	Rd (15.16)			tc in 16 half.
m	Df (17·18)	Pn (17·18)		DS=2·17 WY = 1·18. X=18·13.	c, wt in 17 half; p in 18 half.
m°	Dv (19·19)	Sp (19·20°)		SE=9·20° (10·19). trIx=(20·19·23).	sh. MS in either Sp or Ec.
S°		Gl (21°·22)		(3·21) (4·22). (11·21). (12·22).	sc, bb, pl.
s		Ix (23·24)		trIx=(20·19·23).	sw.

The ends 10°, 12°, 20° and 21° are characterised by terminal humps.

Rl = Rolled
Gs = Glossy
Bk = Bucking
El = Elongate
Ec = Echinus
Ck = Cocklebur
Mc = Microcarpic
Rd = Reduced
Pn = Poinsettia
Sp =
Gl = Glove
Ix = Ilex

Py. = Polycarpic
Sm. = Smooth
St. = Strawberry
Un. = Undulate
Mt. = Mutilated
Wd. = Wedge

Sc. = Scalloped
Df. = Dwarf
Dv. =

Sg. = Sugar loaf

At. =

Th. =

DS =
Wy. = Wiry
Es. =
Ph. = Pinched

Hg. = Hedge
trSg. =
Mp. = Maple
X =
trIx =

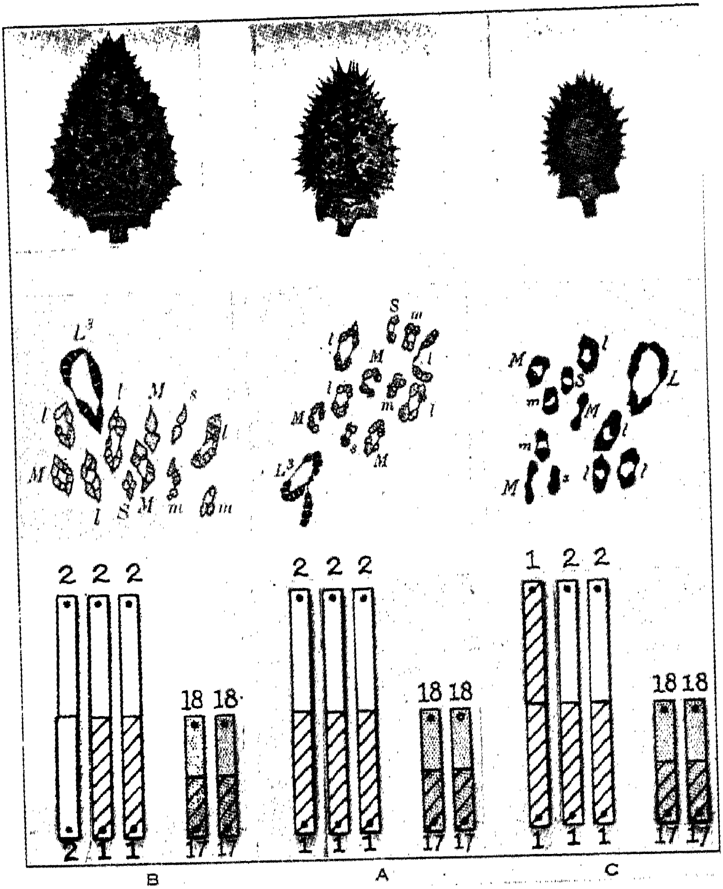


FIG. 33. Capsule form, chromosome complement (metaphase I.) and diagrammatic explanation of the constitution of the trisome in A, the primary trisomic Rolled, B and C the related secondary trisomics Sugarloaf and Polycarpic respectively of *Datura Stramonium*. (Blakeslee, 1930.)

[*To face p.* 238.

On the theory of specificity of pairing a plant with a chromosome constitution, 2·1, 1·1, 1·2 may exhibit a ring of three chromosomes at meiosis. A secondary trisomic of *Datura* having three chromosomes of this constitution will therefore have the following gametic output (the remaining eleven chromosomes of the normal gametic complement are omitted in each case) :—one 1·2 1·2 ($x + 1$ primary "trisomic" gamete) : one 1·1 1·2 ($x + 1$ secondary "trisomic" gamete) : two 1·2 (normal gamete) : one 1·1 (abnormal reduplicated and deficient gamete).

Corresponding to each primary trisomic, two secondaries of the types 1·2 1·2 2·2 and 1·2 1·2 1·1 are expected. Out of the twenty-four expected secondary trisomics in *Datura* fourteen have been found by Blakeslee and his co-workers (see Fig. 32).

Tertiary trisomics consist of two pairs of homologous chromosomes (1·2, 1·2, 5·6, 5·6) and a third chromosome (2·5) consisting of parts of chromosomes 5·6 and 1·2, in addition to the remainder of the chromosome complement.

Tertiary trisomics may result from segmental interchange between one of the trivalent chromosomes and a non-homologous chromosome. Thus, if the original chromosome was 1 · 2 in a primary trisomic, inversion would produce 1 · 1 and 2 · 2 (secondary trisomics) and segmental interchange would produce 1 · 3, 2 · 4, etc., where 3 and 4 are segments of a chromosome not homologous with those of the trivalent.

Table 43 gives a list of the primary trisomics and corresponding secondaries and tertiaries in *Datura*. They are arranged according to the length of the chromosomes of the trisomic set and the genes located in particular parts of chromosomes are also given. The American system of numbering the twenty-four ends of the chromosomes is employed instead of the English system where letters are used.

The tertiary chromosomes, represented by figures in parentheses, are those whose ends are known, but whose morphological effect when present as extras is unknown.

BALANCE

One of the most convincing proofs of balance between factors was given by Bridges (1922) on the sex determination in *Drosophila* *melanogaster.* He proved that the balance between the X chromosome and autosomes (A) is responsible for the sex determination. When the two X chromosomes in diploid flies (sex chromosomes, see p. 74) are balanced by the diploid set of autosomes, the individual is female ($2X : 2A$), and the male is obtained by the upset of the balance between the X and autosomes ($1X : 2A$). The X chromosomes are female determiners and the autosomes (except the fourth chromosome) are male determiners. It is well known that the Y chromosome is concerned with fertility, but not with sex determination (Stern, 1926*a,b*, 1927*a,b*). Alteration of this balance between X and A in plus or minus direction yielded super female $3X : 2A$, intersex $2X : 3A$, and super male $X : 3A$ individuals (see Table 44).

TABLE 44

Relation of Sex to Chromosomes in Drosophila melanogaster. (Bridges, 1922.)

Sex.	X-chromosomes.	Sets of Autosomes.	Sex Index.
Super female	3	2	1·5
Female triploid	3	2	1
Female diploid	2	2	1
Female haploid	1	1	1
Intersex ♀-type	2	3 (−IV)	·67+
Intersex ♂-type	2	3	·67
Male	1	2	·5
Super male	1	3	·33

The trisomics of *Datura*, of tomato (Lesley), of *Matthiola* (Frost (1919), Frost and Mann (1924), Lesley and Frost (1928)), and of maize (McClintock, 1930) give many illustrations of the effects of genic balance and shed considerable light on the genetic constitution of plants and animals.

The morphological changes brought about by the reduplication of an identifiable part of the chromatin confirm the general view of the genetic differences of the parts. Each part of the chromatin content is specifically differentiated genetically.

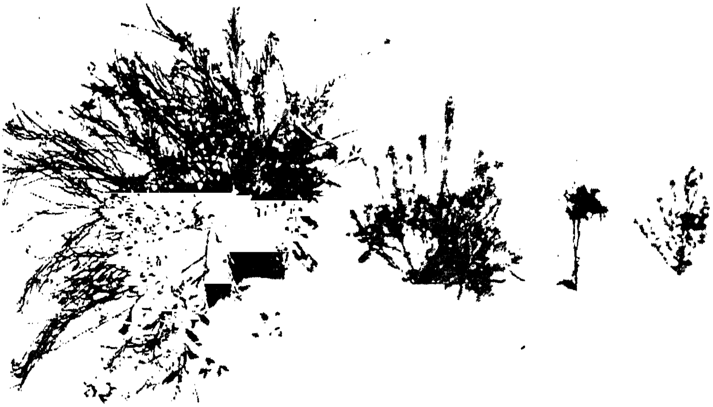


FIG. 34. Normal, trisomic Small, extreme Small (tetrasomic diploid), and extreme Small (disomic haploid) plants of *Matthiola incana*. (Lesley and Frost, 1928.)

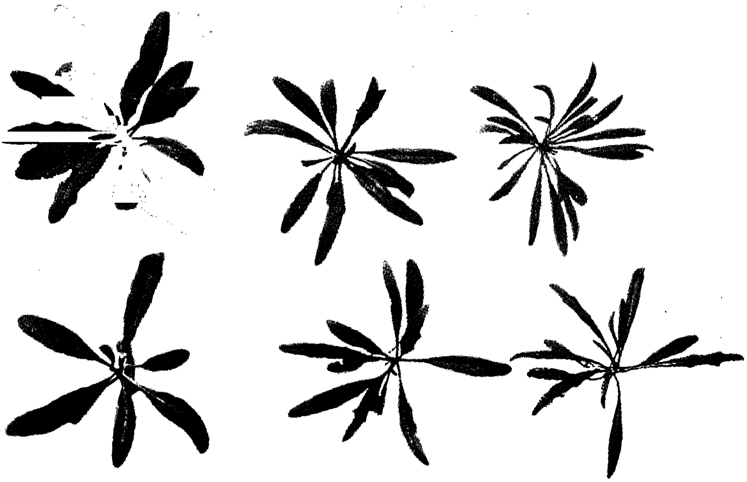


FIG. 35. Types of *Matthiola incana* with one, two and three extra chromosomes. From top left: Normal (14), Slender (14 + 1), extreme Slender (14 + 2); below: Large (14 + 1), Large Slender (14 + 1 + 1), Large extreme Slender (14 + 1 + 2). The "Slender" chromosome makes the leaves narrower; the "Large" chromosome makes the leaves fewer. (Frost, 1927.)

The effect of an extra chromosome, or part of a chromosome, upon character expression is very similar to that of single genes. Indeed, Blakeslee, Avery and Bergner (1935 and 1936), Muller (1935), Muller and Prokofieva (1935), Bridges (1936), Goldschmidt (1937) *et al.* have shown the close similarity in effects. It is obvious therefore that a block of many genes on a part of a chromosome may act on the phenotype like one gene. The effect may resemble that of a known gene although that gene is not carried by the chromosome of the trisome. Thus P, a gene for flower colour in *Datura*, is carried by chromosome 17·18, yet trisomics for 3·4 (Glossy) and 11·12 (Cocklebur) darken and lighten the flower colour respectively. Lesley (for *Lycopersicum*) and Frost (for *Matthiola*) provide further examples of trisomics with contrasting effects.

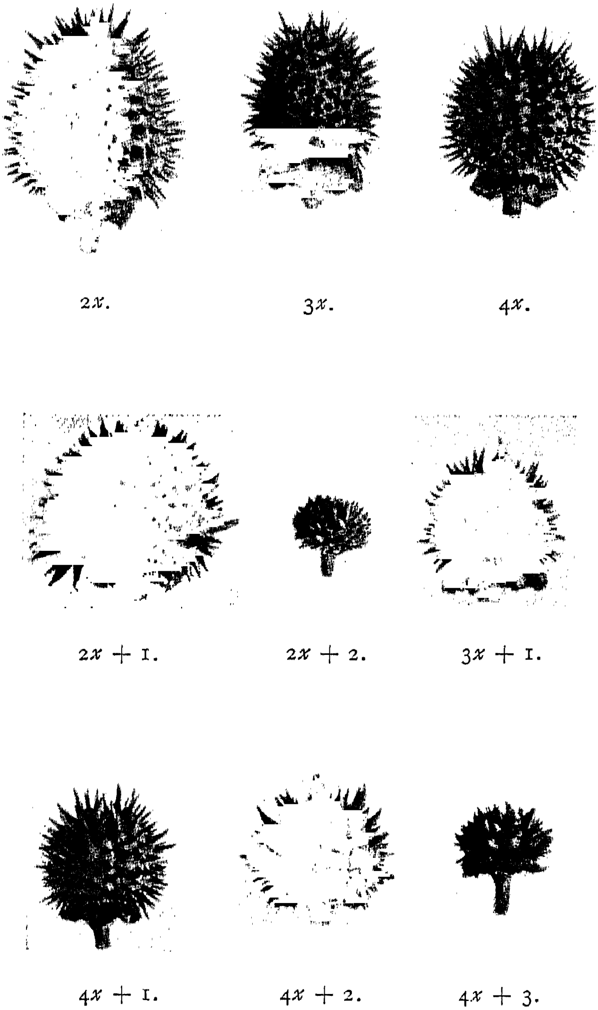
The haplo IVth and triplo IVth *Drosophila melanogaster* containing $2x-1$ and $2x+1$ chromosomes respectively illustrate the specificity of the chromosomes. Characters such as broad wings, rough eyes, pale body colour and small size of the $2x-1$ flies are in contrast with the narrow wings, smooth eyes and dark body colour of the $2x+1$ flies. Normal flies with $2x$ chromosomes are intermediate for these characters between these forms. In the progeny of Small, a trisomic ($2x + 1$ fragment) of *Matthiola*, Lesley and Frost (1928), found two plants with the Small characters intensified. One was ($2x + 2$ fragments) a tetrasomic diploid, and the other was ($x + 1$ fragment) a disomic haploid (see Figs. 34, 35). The equal balance of $2x + 2$ and $x + 1$ is reflected in the similarity of the characteristics. The Globe mutants, involving chromosome 21·22 of Datura, exhibit a range in degree of expression from $4x + 1$, $4x + 2$, $2x + 2$, $4x + 3$ to $2x + 1$. As expected the $4x + 1$ form is least extreme and the $2x + 1$ form most extreme in expression. The number of times the same genes are duplicated in an individual does not have as great an effect as the proportionate number of times the gene is repeated in comparison with the rest of the genetical content. Lesley (1937) finds that the trisomic Ddd tomato is tall, whereas the triploid and tetraploid simplex forms are incompletely dominant. *Drosophila* provides moreover examples of this effect, *e.g.*, Sturtevant and Schultz (1931). Haploid, diploid, triploid, tetraploid and other euploid plants of one species are similar in type, except in a few physiological characters; the size of plant, which apparently does not result from differences in growth rate, the vitamin C content (Crane and Zilva (1932), Sansome and Zilva (1933, 1936)), and the size of individual cells and proportion of tissues may be influenced (generally increased) by doubling of the chromosomes.

The loss of a chromosome from the diploid complement has always a more drastic effect than the addition, while a plant of the constitution $2x + 1 + 1$ is usually more vigorous than one of the $2x + 2$ constitution. In *Datura*, $x + 1$, $2x - 1$, $3x - 1$ and $4x - 1$ forms have been obtained (Blakeslee and Belling, 1924), while nullosomic ($4x - 2$) and monosomic ($4x - 1$) forms are known in *Nicotiana* (see p. 315). In polyploids the addition or loss of a chromosome does not cause so great an effect as in diploids, *e.g.*, wheat and oats ($6x + 1$) ($6x - 1$). (See p. 212.)

Two important aspects of balance have been developed in the last five years. The first relating to the presence or absence of small parts of chromosomes has been utilised in the mapping of chromosomes and will be dealt with later (p. 253). The second relating to the duplication of large parts of chromosomes has been used to produce new and distinct breeding types in *Datura*.

The primary, secondary and tertiary trisomics of *Datura* each have a characteristic effect upon the phenotype of the plant. Thus (see Table 43) a plant $2x + 1{\cdot}2$ has the Rolled characteristics, a plant $2x + 1{\cdot}1$ has Polycarpic characteristics, $2x + 2{\cdot}2$ has Sugarloaf characteristics.

The secondary trisomics are extreme in the expressions of the genes carried by $0{\cdot}1$ and $0{\cdot}2$ respectively, while the primary trisomic is usually intermediate between them. A tertiary trisomic, say $2x + 2{\cdot}17$, will combine the characteristics of $2x + 2{\cdot}2$ and $2x + 17{\cdot}17$ and be less extreme than either in expression. The trisomic " Nubbin " (Blakeslee, 1927*a*,*b*) arose through *X*-raying the parent plant. It is of the constitution $2x - 1{\cdot}2 + 9{\cdot}1 + 2{\cdot}5$, *i.e.*, the two $1{\cdot}2$ chromosomes of the diploid are replaced by three chromosomes which contain the normal balance of $1{\cdot}2$ but in different chromosomes. The duplication of the segments 9 and 5, however, gives rise to the Nubbin characteristics. Incidentally, Nubbin by its constitution should and does give rise to the tertiaries $2x + 1{\cdot}9$ and $2x + 2{\cdot}5$ and the primaries $2x + 5{\cdot}6$, $2x + 1{\cdot}2$, $2x + 9{\cdot}10$. Another " compensating " type is $2x - 1{\cdot}2 + 1{\cdot}1 +$



$2x$. $3x$. $4x$.

$2x + 1$. $2x + 2$. $3x + 1$.

$4x + 1$. $4x + 2$. $4x + 3$.

Fig. 36. Normal diploid, triploid and tetraploid capsules of *Datura Stramonium* are shown above. Below are capsules of forms having one or more extra chromosomes of the Globe set. (Blakeslee, 1930.)

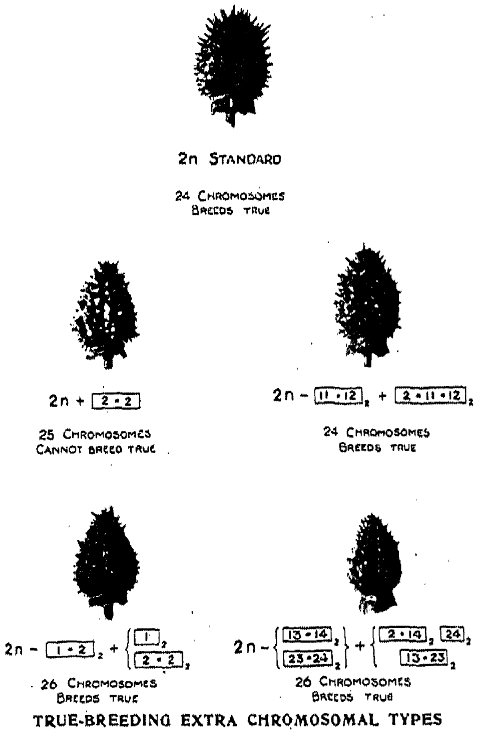

2n Standard
24 Chromosomes
Breeds true
$2n + \boxed{2 \cdot 2}$
25 Chromosomes
Cannot breed true
$2n - \boxed{11 \cdot 12}_2 + \boxed{2 \cdot 11 \cdot 12}_2$
24 Chromosomes
Breeds true
$2n - \boxed{1 \cdot 2}_2 + \left\{ \begin{array}{l} \boxed{1}_2 \\ \boxed{2 \cdot 2}_2 \end{array} \right.$
26 Chromosomes
Breeds true
$2n - \left\{ \begin{array}{l} \boxed{13 \cdot 14}_2 \\ \boxed{23 \cdot 24}_2 \end{array} \right\} + \left\{ \begin{array}{c} \boxed{2 \cdot 14}_2, \boxed{24}_2 \\ \boxed{13 \cdot 23}_2 \end{array} \right.$
26 Chromosomes
Breeds true
TRUE-BREEDING EXTRA CHROMOSOMAL TYPES

FIG. 37. True-breeding extra chromosomal types in *Datura Stramonium*. (Blakeslee, 1930.)

[*To face p.* 243.

2·17 where the extra material is 1·17. These compensating types arise most frequently from a plant having two tertiary chromosomes resulting from segmental interchange (see p. 252). It will be realised that these trisomics will not breed true. By genetical methods, Blakeslee and his co-workers have produced plants (1) of the constitution $2x - 2\ (11\cdot12) + 2\ (2\cdot11)\cdot12$, *i.e.*, with 24 chromosomes and containing 0·2 on 11·12, (2) of the constitution $2x - 2\ (1\cdot2) + 2\ (1) + 2\ (2\cdot2)$, *i.e.*, 26 chromosomes; and (3) of the constitution $2x - 2\ (13\cdot14) - 2\ (23\cdot24) + 2\ (2\cdot14) + 2\ (24) + 2\ (13\cdot23)$, *i.e.*, 26 chromosomes. All types show a similarity to each other and to the $2x + 2\cdot2$ trisomic as they should on the grounds that all three plants are tetrasomic for 0·2 (see Fig 37). Other pure breeding types have also been synthesised with extra material at the ends of the chromosomes. Types with insertion of material have also been produced, mainly as a result of two segmental interchanges between two non-homologous chromosomes at different places followed by crossing over of the products. The phenomenon has been observed cytologically in *Zea* (McClintock) and *Datura*. If, for example, ABCD has two segmental interchanges with XYZ, one producing ABYZ and XCD, and the other ABZ and XYCD, then the hybrid between both can give gametes containing ABYZ, XYCD, where Y, an intercalary segment, is duplicated. These and other phenomena from the important experiments with *Datura* and *Zea* will be dealt with later. Reference should be made to the literature key for further information.

The effect of unbalance on the viability of gametes has already been mentioned in connection with trisomic inheritance. Important work on pollen germination of the various balanced and unbalanced forms of *Datura* has been carried out by Buchholz and Blakeslee (1922, 1927*a*,*b*,*c*, 1924, 1930*a*,*b*), Blakeslee and Cartledge (1926, 1927), Davenport (1924, 1925), Buchholz, Blakeslee and Avery (1935), Buchholz, Williams and Blakeslee (1935). In the gamete, as in the zygote, the degree of unbalance varies with different chromosomes. The extra chromosome in the pollen of the cocklebur trisomic $2x + 11.12$ causes the growth of the pollen tube to be slower than that of a normal pollen tube (see p. 37). The trisomic $2x + 1\cdot2$ produces pollen tubes with $x + 1\cdot2$ chromosomes which burst just below the stigma. The related secondary trisomic $2x + 2{\cdot}2$ produces four types of gamete in the following proportions: $2(x + 2{\cdot}2) : 1(x + 1{\cdot}2) : 1(x - 1{\cdot}2 + 2{\cdot}2)$. The x class of pollen tubes grows normally, the $x + 2{\cdot}2$ class grows at two-thirds the normal rate, the $x + 1{\cdot}2$ class grows slowly then bursts, while the $x - 1{\cdot}2 + 2{\cdot}2$ pollen grains are abortive. It will be noticed that the $x + 2{\cdot}2$ gamete is potentially functional whereas the primary $x + 1{\cdot}2$ is not. The other secondary of $2x + 1{\cdot}2$, namely $2x + 1{\cdot}1$, produces $x + 1{\cdot}1$ pollen grains which do not germinate together with $x + 1{\cdot}2$, x and the abortive $x - 1{\cdot}2 + 1{\cdot}1$ which behave as before.

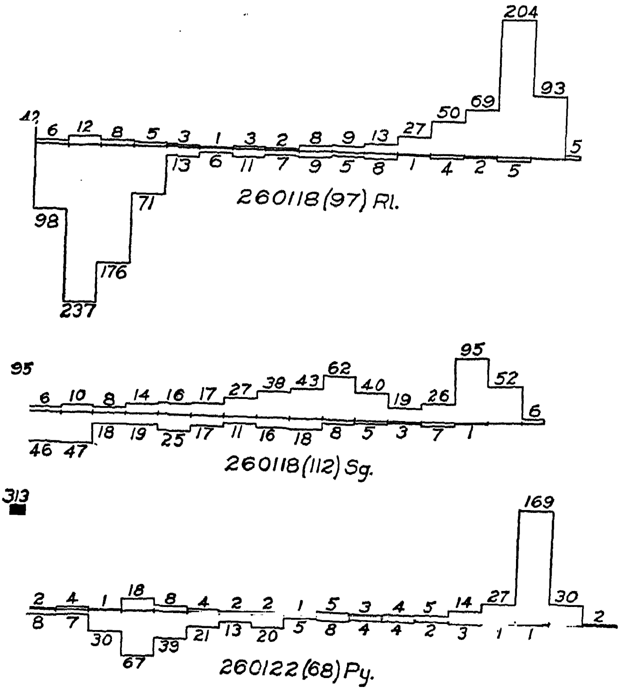


FIG. 38. Diagrams of pollen distribution in tests of the pollen of Rolled (Rl), Sugarloaf (Sg) and Polycarpic (Py). The ends of the pollen tubes were counted and plotted; the spaces on the datum line are 2 m.m. intervals. (Buchholz and Blakeslee, 1930.)

The two parts, 0·1 and 0·2 of the 1·2 chromosome, therefore affect pollen tube behaviour in different ways (see Fig. 38). Buchholz, Blakeslee and Avery (1935) have shown that in a compensating type $2x^2 + (2{\cdot}11{\cdot}12)^2 - (11{\cdot}12)$ the $x + 2$ gametes grow faster than the $x + 2{\cdot}2$ gametes from the secondary trisomic $2x + 2{\cdot}2$. The authors state that the reduction rate of pollen tube growth in comparison with that of x gametes is at least roughly proportional to the amount as well as dependent on the kind of extra material present. The accompanying diagrams constructed by Blakeslee and Buchholz (1930) illustrate the differences in behaviour of pollen grains and pollen tubes of different constitutions.

Chromosome deficiency seems to have the greatest effect on the gamete. Pollen-carrying deficiencies is generally, but not always, abortive or inviable. Stadler (1931) shows that a deficiency in *Zea* is viable, while Muller (1935) indicates their importance and prevalence in *Drosophila*. The presence of duplications of chromosome parts as common and normal constituents of the genotype must always be realised in this connection.

HAPLOIDS

Table 45 summarises the occurrence of haploid plants among Angiosperms. Although the leaves and flowers differ slightly from the female parent in most cases the haploids appear as reduced replicas of the mother plant. (See Fig. 39). For this reason it is believed that with the exception of cases in *Nicotiana*, *Crepis*, and possibly *Triticum*, they have arisen by the parthenogenetic development of the egg-cell.

Origin. The majority of haploids have resulted from the crossing of two distantly related species (see Table 45), and it is considered that the stimulus of the foreign pollen induces parthenogenesis. By pollinating *Solanum nigrum* with *S. luteum* and other species of *Solanum*, Jørgensen (1928) obtained haploids of *S. nigrum*. He observed that the pollen tubes of *S. luteum* entered the embryo-sac of *S. nigrum*, but that the nuclei did not fuse with the egg and endosperm nuclei. The male nuclei degenerated while the egg underwent division and formed the embryo.

Similarly Noguchi (1928) found that when *Brassica campestris* var. *oleifera* was pollinated by *B. oleracea* var. *gemmifera* the male nuclei did not fuse with the egg or polar nuclei but that the male nucleus stimulated the egg to develop into an embryo.

In two cases in *Nicotiana* the haploid plants had the haploid chromosome number of the male parent and also resembled the male parent. *N. digluta* ($2n = 72$) × *N. Tabacum* ($2n = 48$) gave a plant like *Tabacum* having 24 chromosomes, Clausen and Lammerts (1929). *N. Tabacum macrophylla* ($2n = 70$–72) × *N. Langsdorffii* ($2n = 18$) gave a plant like *Langsdorffii* having 9 chromosomes, Kostoff (1929). It is concluded that here the embryo developed from the male nucleus in the egg cytoplasm (haploid merogony). Diploid merogony is not uncommon in *Nicotiana* interspecific crosses.

Low and high temperature and X-rays also have been used to stimulate the production of haploids, while Kappert in *Linum*, Harland in *Gossypium*, and Müntzing in various *Gramineæ* have shown that one embryo of twin seeds is haploid in a frequency which is higher than normal. 211 haploid plants have been found in *Datura* (Blakeslee and Satina, 1937) who have shown that haploids appear as frequently in inbred lines as they do in hybrids.

An example of the spontaneous origin of a haploid was found by Lindstrom (1929), who discovered a haploid tomato among the F_2 progeny of an intervarietal cross.

Cytology. Chromosome pairing and chiasma formation at meiosis depend on the homology of the chromosomes. In true haploids the chromosomes are all different from one another, *i.e.*, they are non-homologous and no pairing takes place The unpaired chromosomes either segregate at random to the opposite poles and divide equationally at the second division or they may divide at the first division, when the second division will usually be suppressed, *i.e.*, non-reduction. In the *Œnothera franciscana* haploid Davis and Kulkarni (1930) found that often only one pole to the spindle was formed, the chromosomes did not split, and hence the first division was suppressed. Fusion of two or more pollen mother cells in the wheat haploid was observed to give rise to pollen grains with a high number of chromosomes. In the somatic cells of the ovary fusion of two nuclei often occurred and binucleate cells were very frequent. This is comparable with somatic doubling in *Solanum* (Jørgensen, 1928, etc.).

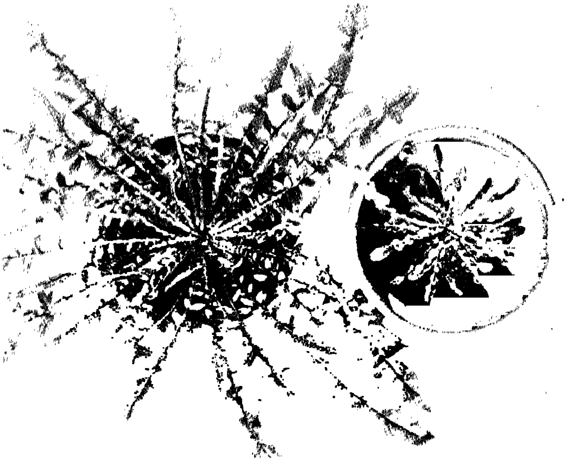


FIG. 39. Diploid and haploid plants of *Crepis capillaris* of the same age. (Hollingshead, 1930*c*.)

FIG. 40. Microphotographs of metaphase I. in haploid *Œnothera blandina* showing pairing of chromosomes. (Catcheside, 1932.)

[*To face p.* 246.

Solanum nigrum is a hexaploid with 72 chromosomes and in the "haploid" with 36 chromosomes Jørgensen found that from 3 to 12 bivalents were formed. This suggests that 2 of the 3 sets of chromosomes of the haploid are sufficiently alike to pair and presumably are of similar phylogenetic origin. It also provides strong evidence that *S. nigrum* is an allohexaploid.

Œnothera franciscana at first metaphase in meiosis forms 5 bivalents and a ring of 4 chromosomes. Emerson (1929) finds that in the haploid 2 "bivalents" are frequently formed. Catcheside (1932, 1933) also observed pairing of chromosomes in the haploid of *O. blandina* (see Fig. 40).

Davis and Kulkarni also show 2 bivalents in their drawings, although they state that no pairing takes place. Pairing of chromosomes in haploid *Œnothera* is not surprising in view of the structural hybridity of the species (see p. 271).

The consequence of irregularities in meiosis is that unreduced gametes and gametes with chromosome numbers ranging from one to the unreduced number are frequently formed. Those with less than the unreduced chromosome number (*i.e.*, with deficiencies) are inviable, due to unbalance (see p. 243). This accounts for the characteristic sterility of haploids. Only the unreduced gametes are viable, and the percentage of non-reduction varies in different haploids. In the *Matthiola* haploid, which incidentally is a disomic haploid (see p. 241), there is 70% non-reduction, whereas in *Datura* there is from 10% to 29%. Unreduced pollen grains are usually about the same size as pollen grains of a normal diploid plant.

Genetical Behaviour. Where selfed progeny of haploids can be obtained, it follows that they consist mostly of plants with the diploid chromosome number. Haploids are therefore particularly valuable for the production of diploids which are homozygous in every respect. This, of course, does not apply to haploids of structural hybrids or to some polyploids.

The selfed progeny of *Datura* haploids consist mainly of diploids, but 3·05% are trisomic ($2x + 1$) forms. The frequency of trisomic forms in the progeny of haploids is therefore much greater than in the progeny of normal diploids (0·47%), or of trisomic ($2x + 1$) parents (1·11%). Blakeslee, Morrison and Avery (1927) point out that these trisomic forms may result from non-reduction in the first division followed by non-separation in the second division or else by somatic non-separation at some stage between gamete formation and the early development of the zygote. Many of the balanced chromosomal types and primary and secondary trisomics have been derived from haploid *Datura.*

The haploid *Œnothera franciscana* on selfing gave typical diploid *franciscana* and a few other forms. A few haploids were also produced, again parthenogenetically. Back crossed with diploid *franciscana* ordinary diploid *franciscana* progeny were obtained (Davis and Kulkarni, 1930). Similar results were obtained by Stomps (1930*a*). The aberrant forms he observed were like the 3*x semigigas* and the trisomic mutants *scintillans* and *lata.*

An interesting fact is that *O. Hookeri,* a homozygote which is closely related to *O. franciscana,* has given haploids almost identical with and in the same frequency as those from *franciscana.* The *Hookeri* haploid, however, was completely sterile.

When pollinated by a normal diploid the tomato haploid gave normal diploid progeny.

Several gene mutations at a frequency of 1·35% of the progeny, and disomic haploid plants ($1x + 5{\cdot}5$, and $1x + 7{\cdot}7$) have been found in *Datura* (Satina and Blakeslee and Avery, 1937). Davis and Kulkarni have evidence of possible gene mutation in the progeny of haploid *O. franciscana.* It may be that these mutants and some of the other mutants in the progeny of haploid *O. franciscana* are the result of pairing of chromosomes which do not normally pair in the diploid. The possibility of crossing-over thus provided may lead to a change in the genetical constitution of the chromosomes.

Somatic cells of the root tips of haploids commonly mutate to the diploid condition. These diploid cells are usually larger than the haploid cells. Haploid *Crepis capillaris* and *Datura* plants have also been observed to form branches of diploid and haploid tissues (periclinal chimæras) (Hollingshead, 1930*c*). Pollen mother cells of haploids are about half the volume of those of the corresponding diploids. See Ivanov (1938) for a review of haploids.

TABLE 45

The occurrence of haploids in Angiosperms

Species.	Origin.	Chrom. No.	Chromosome behaviour in p.m.c.	Progeny.	Authority.
Brassica Napellus	Spontaneous.	19	0–711 *m*	—	Morinaga and Fukushima (1933). "Cytologia."
Crepis	Hybrid.	3	I *m*	Somatic doubling.	Hollingshead (1928, 1930), Babcock and Navashin (1930).
	Normal pollen.	4	— *m*	,,	Gerassimova (1936).
	X-rayed ovaries.		*p*	,,	
Datura	1. Low temperature. 2. Species hybrid.	12	Im *m*	Somatic doubling. Aneuploids. Euploids.	See literature key.
Gossypium	1. Spontaneous. 2. Twin embryo.	26	— *m*	X *G. armourianum* ($2n \times 26$) gave hybrid.	Harland (1936), *Journ. of Heredity*.
	3. Species hybrid.	13	— *m*		Skovsted (1935), *Journ. of Genetics*.
Lycopersicum	Spontaneous.	12	I *m*	Gametic doubling.	Lindstrom (1929), Lindstrom and Koos (1931).
Matthiola	$(2n + 1fr) \times 2n$.	$7+fr$	I *m*	—	Lesley & Frost (1928).
Nicotiana glutinosa	1. Spontaneous pure line 2. mF_2 from X-ray aberrants.	12	I *m*	—	Goodspeed and Avery (1929).

* = New type. *m* = Maternal type. *p* = Paternal type.

Species.	Origin.	Chrom. No.	Chromosome behaviour in p.m.c.	Progeny.	Authority.
N. Langsdorffii . .	*N. Tabacum* × *N. L.*	9	" II " & I *p*	—	Kostoff (1929).
N. rustica . .	1. By X-rayed pollen. 2. By *N. Tabacum*.	24	I *m*	2*n*	Ivanov (1938), *Genetica*.
N. sylvestris . .	*N. Tabacum sylvestris* × *N. sylvestris*.	12	" II " & I *p*	—	Kostoff (1934), *Nature*.
N Tabacum . .	In species hybrid.	24	I & " II " *m* or *p*	2*n*	Clausen and Morn (1924), Chipman and Goodspeed (1927), Ruttle (1928), Clausen and Lammerts (1929).
Œnothera . .	Spontaneous.	7	I & II *m*	—	Stomps (1930).
argillicola . .	Species hybrids.	7	,,	2*n* and *n*	Catcheside (1932), Davis and Kulkarni (1930) Anderson (1933), Blair (1933), Stomps (1930), Gates and Goodwin (1930).
blandina . .	,, ,,	7	,,		
franciscana .	,, ,,	7	,,		
Hookeri . .	,, ,,	7	,,		
rubricalyx . .	,, ,,	7	— *m*		
Oryza sativa . .	Spontaneous, twin seeds.	12	I & II *m*	2*n*	Morinaga and Fukushima (1934), *Jap. J. of Bot.*
Pharbitis Nil . .	Spontaneous.	15	I & II *m*	—	Katayama (1935), *Jap. J. of Genetics*.

Portulaca grandiflora	F$_2$ specific hybrid.	9	I *m*	Gametic doubling	Okuma (1933), *Jap. J. of Genetics*.
Solanum nigrum	1. Self pollinating a chimæra. 2. × *S. luteum*.	36	12 II=12 I *m*	Gametic doubling	Jørgenson (1928).
Triticum monococcum	1. Spontaneous.	7	I occ. II *m*	*n* and 2*n*	Katayama (1935), *Jap. J. of Botany*.
	2. × X-rayed pollen.	—	4	—	Chizaki (1934) *Bot. Mag., Tokio*.
dicoccum	× X-rayed pollen.	14	— *	—	Yafeikin and Vasiljiv (1936), *Bull. Appl. Bot. and Gen. U.S.S.R.*
persicum	,, ,,	14	—	—	Do. do. do.
durum	× *T. monococcum*.	14	— *p*	—	Vasilyiv (1936), Ivanov (1938) (see *Genetica*).
turgidum	× Secale cereale.	14	— *m*	—	Nakajima (1935), *Jap. J. Genetics*.
compactum	× *Ægilops*	21	I & " II " *m*	—	Gaines and Aase (1926).
vulgare	1. Twin seedlings 2. Spontaneous.	21	I II III *m*	—	Yamasaki (1936), *Jap. J. Bot.*
Zea Mays	1. Spontaneous.				
	2. × X-rayed pollen.	10	I *m*	—	Stadler (1931).
	3. Heat.	—	—	—	Randolph (1932).

* = New type. *m* = Maternal type. *p* = Paternal type.

CHAPTER IX

STRUCTURAL HYBRIDITY

Segmental Interchange — Translocations — Duplications and Deficiencies —Inversions—Œnothera.

Introduction. The recently acquired knowledge that chromosomes may undergo changes in structure at a comparatively high frequency has had a considerable effect on genetical thought. Our views on balance, position effect, mutations, sex determination, variegation, as well as our interpretations of autosyndesis, secondary pairing and chromosome relationships, have been greatly influenced by the new knowledge.

Segmental Interchange. The hybrid between two phenotypically similar disomic races of species of *Datura*, *Zea*, *Pisum*, *Œnothera*, *Drosophila* and other species may form a ring of four or more chromosomes. Belling (1925*a*), Blakeslee and Belling (1926) had suggested that the ends of two non-homologous chromosomes had interchanged positions in one parent of the hybrid. Thus one race would have the chromosomes 1·2, 17·18, whereas another race would have the parts of these chromosomes arranged 1·18, 2·17. If pairing only takes place between homologous parts, the hybrid would form a ring: 1·2, 2·17, 17·18, 18·1. This explanation is now generally accepted. The occurrence of an association of more than two chromosomes in a diploid or of more than four in a tetraploid implies that segmental interchange (reciprocal translocation) has taken place between non-homologous chromosomes. Darlington's (1929) paper on the genetical and cytological results in *Œnothera* (see p. 264) and McClintock's data 1930, 1931, 1933, have furnished us with considerable evidence for the theories of pairing of homologous parts and of interchange of chromosome parts.

McClintock has observed that pairing may take place between homologous parts of chromosomes and non-homologous parts, but that the latter does not persist from prophase to metaphase and is therefore not important in segregation. The pairing in twos of homologous parts in a structural hybrid leads to a configuration such as Fig. 41*a*, where in favourable cases the position of the point of interchange indicated by the change in partners can be identified.

The literature key contains references to a few of the species in which rings of chromosomes resulting from previous reciprocal translocations have been found.

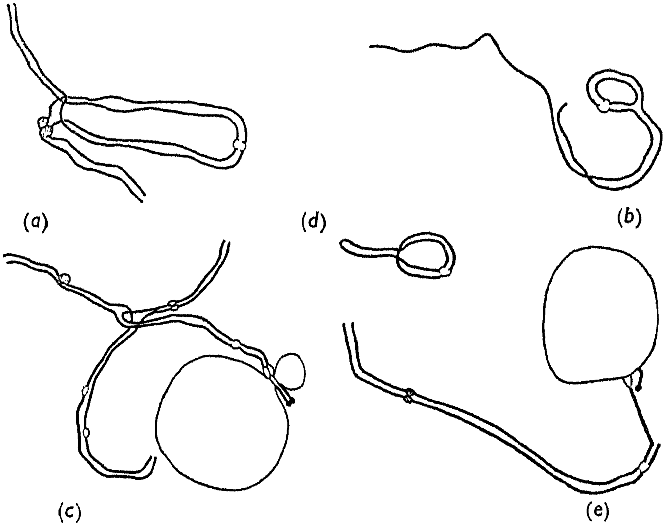


FIG. 41. Prophase configurations in *Zea Mays*: (*a*) Mid-prophase, pairing of a normal chromosome with a homologue containing an inversion. (*b*) Normal and ring chromosomes in homologous association; note non-homologous association of parts of normal chromosome. (*c*) Pairing in reciprocal translocation T4—6. (*d*) Two ring chromosomes of unequal size in association. (*e*) Pairing of a normal satellite chromosome and a chromosome deficient for most of the short arm. (After McClintock, 1931, 1932.)

It is probable that translocation occurs at prophase in a manner similar to crossing-over. McClintock (1931, 1933), observed pairing of non-homologous parts of chromosomes. The chances of non-homologous parts pairing are obviously greater in a plant, such as a haploid or trisomic, with an irregular chromosome complement. McClintock suggests that the folding back of a chromosome on itself which is common in these irregular forms gives greater opportunity for interchange between non-homologous parts ; it is well known that structural changes are more common in the progeny of such plants with irregular chromosome numbers. The secondary trisomics of *Datura* or *Zea*, Rhoades (1933, 1938) ; the fragments or altered chromosomes in *Matthiola*, Frost (1931), Lesley and Frost (1928), Philp and Huskins (1932), Armstrong and Huskins (1934) ; in *Nicotiana*, Clausen (1930, 1931*a,b*) ; in *Lycopersicum esculentum*, Lesley and Lesley (1932) ; and in *Zea*, McClintock (1933), may have arisen in this way. Interlocking of chromosomes as in *Œnothera*, Catcheside (1931), Darlington (1931) ; *Campanula*, Gairdner and Darlington (1932) ; *Allium*, Levan (1933) ; *Pisum*, Pellew and Sansome (1931) ; *Lilium*, Mather (1935), may also lead to interchange, since two non-homologous bivalents are brought into close approximation by entwining and subsequent chiasma formation at prophase. The presence of small duplications or small translocations which are commoner than was at one time thought, may lead by rare crossing-over to segmental interchange. Changes also may occur during mitosis as shown by the ring-chromosomes of *Zea* (McClintock, 1930, 1938) which do not remain constant in the amount of their material throughout one plant's life.

Morphological study of the chromosomes sometimes provides evidence that segmental interchange has taken place. (McClintock (1930), Cooper and Brink (1931), Bergner and Blakeslee (1935), Blakeslee, Bergner and Avery (1936)). For example, in normal maize there is a pair of small chromosomes with knob-like structure at one end. In plants with a ring of four chromosomes resulting from crossing T 8–9*a* with a normal line, two chromosomes had knobs and two were without knobs, but one of the knobbed chromosomes was much larger than the other. The knobless chromosomes also differed in length.

Cooper and Brink (1931) examined a ring of four chromosomes in T 1–6*a* × normal, where a chromosome with trabants is involved. The relative sizes of the segments *AB*, *BC*, *CD*, *DA* of each chromosome are shown in Fig. 41*c*, together with the method of pairing at pachytene. Sometimes from natural sources but mainly from X-rayed material many such segmentally interchanged lines have been obtained. Anderson (1935) reports 64 cases in *Zea*, Bergner, Satina and Blakeslee (1933) report 53 analysed cases in *Datura* (see also Bergner and Blakeslee (1935), Blakeslee, Bergner and Avery (1937)) and Sansome, E. R. (1937, 1938) reports 7 analysed cases, all from natural sources in *Pisum*. If the part interchanged is short, obviously a chain of four chromosomes will be formed in place of a ring. Burnham (1931) reports such a case in maize where the **P–l** chromosome underwent a reciprocal interchange with the **Y–pl** chromosome involving at most only 2 chromomeres of the satellite of the latter chromosome. As stated earlier it is probable that simple translocations are very rare while reciprocal translocations are more common. Work in these genera is proceeding on many other structural changes. Reference should be made to the papers by Hammerlund, Håkansson, Richardson, E., Sansome, E. R., Nilsson, E. on *Pisum*; Anderson, Brink, Burnham, Cooper, Creighton, McClintock, Rhoades on *Zea*; and to the Literature Key on *Datura*. The terminology varies with the genus which is being studied. In *Datura* "prime type," "B race," "cryptic type" refer to the homozygous line interchanged in chromosome segments with respect to a standard line "Line 1." This line 1 has chromosomes 1·2, 3·4, 5·6, etc., while the prime type may have chromosomes 1·3, 2·4, 5·6, the hybrid between them forming the ring 3·1, 1·2, 2·4, 4·3. In maize the earlier workers used the term "semi-sterile" for the hybrid and for the derivative interchanged line but now use the symbols $T1\text{–}2_a$ to indicate that the interchanged line has parts of chromosomes 1 and 2 interchanged. The sub-letters differentiate the different translocations between the two chromosomes.

These terms indicate several of the characteristics of such forms. The interchanged line is usually indistinguishable morphologically from the standard line (cryptic type), and the hybrid between the interchanged and normal lines frequently shows semi-sterility. Paternally and maternally derived chromosomes alternate in the ring of chromosomes. If therefore alternate chromosomes pass to the same pole at metaphase the paternal and maternal types will be recovered in the gametes and the latter will be fertile. When adjacent chromosomes pass to the same pole (non-disjunction) duplication and deficiency of the chromosome segments result, *e.g.*, 1·2, 2·3 leading to gametophytic abortion. Dobzhansky (1933) has been able to genetically analyse the non-disjunction of a ring of four chromosomes resulting from a reciprocal translocation between the II and III chromosomes of *D. melanogaster*. The arms of the chromosomes in the ring are approximately equal. He shows that in this ring 1·2, 2·3, 3·4, 4·1 the proportions are regular disjunction (1·2, 3·4) 1·0 ; non-disjunctional type (1·2, 2·3) 0·47 ; non-disjunctional type (1·2, 4·1) 0·43, or in percentages 52%, 25%, and 22·3%. This corresponds quite well with the discovered 50% pollen abortion found in plants. The reasons for equality in disjunction and non-disjunction have not yet been analysed. If random separation took place we expect 33⅓% of disjunction. It therefore would appear that the orientation on the metaphase spindle as a zig-zag or circle is at random to give 50% disjunction followed by a random orientation of the circle to give equal numbers of the two non-disjunctional types 1·2, 2·3 and 1·2, 4·1. Rings with different relative positions of the centromeres require genetical analysis before the causes of this phenomena can be determined. In *Pisum* and *Zea* 50% abortion of pollen is usually found, while Håkansson (1931) found 50% disjunction in 610 rings of four in *Pisum*. In *Datura* (Bergner, Satina and Blakeslee, 1933) the occurrence of non-disjunction, and hence sterility, is less.

The value of structurally changed forms for genetical analysis is great since the knowledge of the location of genes on the chromosomes, and of the behaviour of duplications and deficiencies for known genes and the creation of new pure breeding forms may be comparatively easily obtained.

It is obvious that, if segments of non-homologous chromosomes are interchanged, the linkage relationships of the genes carried by these segments will be changed. There are three possibilities :—

(1) If the two pairs of allelomorphic genes are situated on different chromosomes in both normal and interchanged lines, *e.g.*, on the *B* and *D* segments of the normal line *AB*, *CD*, and the interchanged line, *BC*, *DA*, pseudo-linkage (Rhoades, 1933), chromosome linkage (Sansome and Philp, 1932), may be shown. The viable gametes will only be those corresponding to the original lines. Hence of the genes contributed by the ring of four, those of each parent will be recovered in one group unless crossing-over has occurred. With crossing-over, the extent of chromosome linkage is measured by the sum of the cross-over values of the distances

between each gene and the point of interchange (usually symbolised Tr).

(2) If the two pairs of genes are located on the different segments of one chromosome in the normal line which are separated in the interchanged line, there will be a combination of true and pseudo-linkage shown by the hybrids. For example, the genes are on *A* and *B* in the normal line *AB*, *CD* and interchanged line *BC*, *DA*.

(3) If the two pairs of genes are on separate chromosomes in the normal line and on one chromosome in the interchanged line. This is the reciprocal of (2) and behaves in a similar manner.

In all three possibilities it will be seen that the point of interchange is a critical point for the control of the linkage value. The linkage map of a ring of four is in the form of a cross with the arms proportional to the length of the segments and with the centre of the cross at the point of interchange (see Fig. 42).

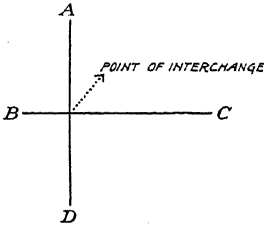


FIG. 42. Diagrammatic representation of the linkage map of a ring of four chromosomes.

Genetical investigations have been made on ring-forming hybrids in *Zea*, *Pisum*, *Datura* and *Œnothera*. Hammerlund (1928) was the first to report an experiment on such hybrids in *Pisum sativum*. **A**, a gene for flower colour and **Gp** for green pod are inherited independently in a normal line, but were found to be linked in the hybrid between the normal and an interchanged line. It was not possible to say from the results whether genetical linkage or pseudo-linkage is involved since it was unknown whether the interchanged line itself showed linkage between **A** and **Gp**. Pellew and Sansome found in hybrids between a Tibetan variety and a commercial strain that those plants heterozygous for the allelomorphs round (**R**) and wrinkled (**r**), had a ring of four chromosomes and 50% gametic abortion, while the plants homozygous for round and wrinkled had no ring and no sterility. Analysis of the families showed that a small proportion of the homozygotes had rings and sterility and a small proportion of the heterozygotes (**Rr**) had no rings.

If we suppose that the factors **Rr** are located in the ring of chromosomes and that crossing-over takes place between the locus of **R** and the point of interchange, then an interchanged line with the factors **RR** and a normal line with the factors **rr** will be formed. These on hybridisation with the original lines will give semi-sterile homozygotes and fertile heterozygotes.

In maize Brink (1929*b*), McClintock (1930), McClintock and Hill (1930), Creighton and McClintock (1931), and Rhoades (1931), have identified the linkage groups which were involved in the rings in the lines semi-sterile 1, 2 and 4.

The chromosomes in the ring of T8–9*a* × normal contained the linkage group **C**—**wx**. The chromosomes in the ring of T1–2*a* contained the linkage groups **P** – **br** and **b** – **lg**, and T2–5*a* had **b** – **lg** and **pr** – **v2** linkage groups in the ring. The points of interchange in T8–9*a* and T2–5*a* were known in relation to the loci of the factors of these linkage groups. In the case of T8–9*a* the position of the factors **C**, **sh** and **Wx** were known in relation to the point of interchange and also to the knob-like structure which was mentioned earlier.

It will be remembered that the interchanged chromosomes bearing the knob-like structure are different in length from the knobbed chromosome in the normal races; therefore they can be cytologically identified. There are normal races which do not have the knob-like structure on the homologous chromosome. Creighton and McClintock crossed a plant, semi-sterile and heterozygous for the interchange chromosome (knobbed interchange — knobless normal) with a normal plant (homozygous for knobless) and obtained the following chromosome types in the progeny:—52 knobless normal — knobless normal, 47 knobbed interchange — knobless normal, 37 knobbed normal — knobless normal, and 28 knobless interchange — knobless normal.

The first two categories are similar to the types of the normal and semi-sterile parents respectively, while the last two types are different and constitute the results of crossing-over between the point of interchange and the knob. These figures give the cross-over percentage between the knob and the point of interchange as 39%.

The factor **C** and the knob are closely linked while Burnham (unpub.) *ex.* McClintock (1931) gives the cross-over percentages between the point of interchange and **C**, **sh** and **Wx** as 33%, 32% and 13% respectively.

We have thus a useful method of identifying the position of the factors on the chromosomes in relation to definite visible points.

Similarly, Rhoades (1931) has found that the cross-over percentages between the point of interchange and several factors in T2–5*a* were :—

$\mathbf{b} - \mathbf{lg}$ *linkage group*
$\mathbf{lg}_1 - \mathbf{tr} = 44{\cdot}2\%$
$\mathbf{gl}_2 - \mathbf{tr} = 31{\cdot}3\%$
$\mathbf{b} - \mathbf{tr} = 22{\cdot}0\%$
$\mathbf{ts}_2 - \mathbf{tr} = 4{\cdot}5\%$
$\mathbf{v}_4 - \mathbf{tr} = 7{\cdot}3\%$

$\mathbf{pr} - \mathbf{v}_2$ *linkage group*
$\mathbf{v}_2 - \mathbf{tr} = 50{\cdot}8\%$
$\mathbf{pr} - \mathbf{tr} = 19{\cdot}3\%$
$\mathbf{bt}_1 - \mathbf{tr} = 1{\cdot}5\%$
$\mathbf{bm}_1 - \mathbf{tr} = 1{\cdot}5\%$

Rhoades (1931, 1933) gives the results from a reciprocal translocation between chromosomes 2 and 5 in maize. The genes $\mathbf{v}_2$ and **pr** on chromosome 5 and **b** on chromosome 2, and the point of interchange showed linkage. An important factor is that pairing and crossing-over, although reduced slightly in the neighbourhood of the interchanges, are not greatly interfered with. This indicates that there is remarkable facility in pairing of chromosome parts. Indeed, the genetical evidence is more accurate than the cytological observations which show that the place of change of partners " slides " from the actual point of interchange and creates difficulty in observing the exact point of interchange.

Reduction in crossing-over in the arm in which the translocation occurs has been found in *Drosophila* (Dobzhansky (1930, 1931, 1932), see Table 16). In maize Rhoades (1933) also finds a similar reduction in T2–5*a* heterogyzotes.

This shows that the point of interchange lies close to $\mathbf{ts}_1$ in the $\mathbf{b} - \mathbf{lg}$ chromosome, while in the $\mathbf{pr} - \mathbf{v}_2$ chromosome more factors are required to locate the exact position of the point of interchange in relation to the factor loci.

Rings of Six Chromosomes. In *Pisum sativum*, E. R. Sansome (1932, 1937), in *Zea Mays*, McClintock (1930), Cooper and Brink (1931), in *Campanula persicifolia*, in *Œnothera*, Gairdner and Darlington (1931, 1937) and in *Datura*, plants have been produced with rings of six chromosomes by hybridisation of two plants with rings of four, or of the interchange homozygotic parents.

In maize, T1–2*a* contains the **b** – **lg** and **P** – **br** linkage groups in the ring of four, while T2–5*a* 4 contains **b** – **lg** and **pr** – $\mathbf{v}_2$. The chromosome carrying **b** – **lg** is common to both. In terms of homologous segments the heterozygous lines may be represented as *AB BC CD DA EF EF* and *AB AB CD DE EF FC* where segments *C* and *D* carry the **b** – **lg** linkage group. Fig. 43 illustrates the possible constitutions of the progeny :—

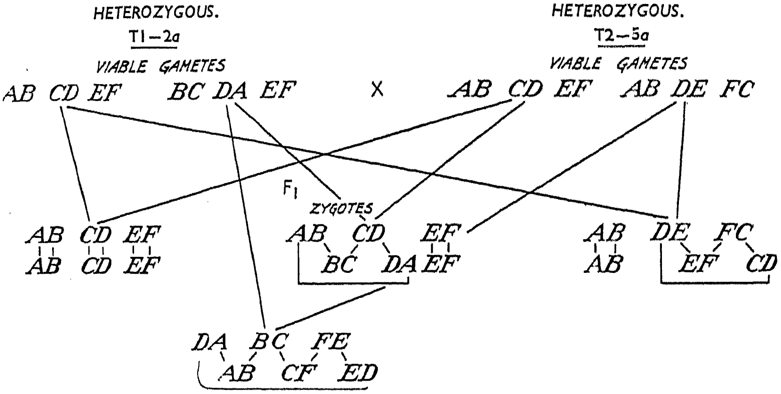


FIG. 43. Constitutions of the possible viable gametes and zygotes resulting from a cross between two lines with different rings of four chromosomes.

We expect therefore a ratio of two plants similar to the semi-sterile parents ; one plant with the normal complement of chromosomes : one plant with a ring of six chromosomes. This latter type was identified by the fact that the sterility of the plant was slightly less than 75% instead of 50%. Similarly Burnham (1930) finds that a plant with a ring of six chromosomes is formed in the progeny of the cross T1–6*a* × T1–2*a*. This indicates that T1–6 contains either the **P** – **br** or **b** – **lg** linkage group in the ring of four. On the other hand, when T8–9 is crossed with T1–2*a* plants with two rings of four and a sterility of slightly over 75 % are obtained. Hence T1–2 and T8–9 do not have a linkage group in common in their rings.

Gairdner and Darlington have shown that four strains of *Campanula persicifolia* from different sources were normal in segment structure while three contained rings of four chromosomes.

Two of these strains, Gm1 and Gm2, had a chromosome in common in the rings, since the hybrid between them had a ring of six. Another hybrid had two rings of four indicating that the chromosomes involved in both rings were distinct. Rings of 10 in *Zea* and *Campanula* and of 8 in *Pisum* have been synthesised by suitable crosses using the double interchange homozygote as one parent. (Gairdner and Darlington (1938), Anderson (1935), Sansome, E. R. (1937)).

These forms with segmental interchanges are excellent material for aiding genetical analysis, in that the content of genes of the segments interchanged may be identified. Further, tertiary trisomics are common derivatives of such forms and the synthesis of segmental interchange heterozygotes is useful in genetical work. The analysis of such forms has indicated the nature of the natural structural hybrids of the *Œnothera* species.

Deficiencies, duplications, simple translocations, inversions and other structural changes are probably to be found in any organism if they are looked for. Their importance is only partly realised, and the workers on *Drosophila* and maize are at present producing data which are changing the fundamental basis of genetics. Bridges (1935, 1936, 1938), Painter (1934), Muller (1935, 1936), and many others are showing that parts of the chromosomes of *D. melanogaster* are " repeats " or small duplications of other parts, and that position effect (see p. 127) and structural changes may simulate genes in their action. For example D (and its allelomorph D_3) Dichæte, a long-known character, is shown to be associated with an inversion. Consequently, many linkage data utilising Dichæte are rendered useless, since the inversion will reduce crossing-over in its neighbourhood. Such characters as Bar, Notch, facet, split, and phenomena relating to Plum and Brown, White and other loci, have been shown to be correlated with structural changes. The identification of structural changes is not so easy in plants as in *Drosophila*. McClintock (1931, 1933, 1938), Creighton and McClintock (1931), Brink and Cooper (1932), Stadler (1933), in *Zea*, Sansome, E. R. (1932, 1937, 1938) and Sutton (1935), in *Pisum*, Nishiyama, Philp (1934, 1938), in *Avena*, Clausen (1930, 1931), in *Nicotiana*, Blakeslee and his co-workers in *Datura*, and others have observed genetical and cytological phenomena resulting from structural changes. Darlington (1937, pp. 159, 273) lists many structural changes in different organisms. (See literature key.)

Inversions (see Richardson, 1936). The inverted section of a chromosome may or may not involve the centromere. If the inversion is terminal (probably a rare occurrence) and crossing-over occurs in the inverted region of a chromosome *AB* the gametic output will be *ABA*, *B*, *AB*, *AB* (see Fig. 44), *i.e.*, a chromosome duplicated for the non-inverted region, a chromosome deficient of the non-inverted (non-viable) and the original chromosomes. If the attachment is in region *A*, the result will be a chromosome without an attachment (*B*), a chromosome with two centromeres *ABA*, both probably inviable, and two original chromosomes. If the centromere is in the inverted region *B* there will result a chromosome duplicated for *A*, a chromosome deficient for *A* and the two original chromosomes.

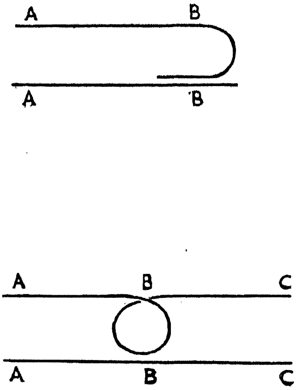


FIG. 44. Diagram of inversions.

If the inversion is intercalary in *B* of the chromosome *ABC* there results *ABA*, *CBC*, *ABC*, *ABC*. If *B* carries the centromere, two duplicated chromosomes *ABA* and *CBC* are produced together with *ABC ABC*. If the centromere is in *A* we obtain *ABA CBC*, *i.e.*, one chromosome with two centromeres and one with no centromere—both probably will not survive. Chromatin bridges at meiotic metaphase I are usually indicative of inversions as the result of one resultant chromatid bearing two centromeres.

Duplications and Deficiencies. Duplications and deficiencies may arise from inversions, from reciprocal translocation and from abnormal crossing-over or from other duplications. Belling (1927) is of the view that structural changes may occur as the result of abnormal crossing-over involving other than homologous parts. The high frequency of breaks in the inert region of the *Drosophila* chromosomes and the repeated origin of one particular inversion suggest that homology, as in the "repeats" of Bridges may have some directive influence. It is significant that simple translocations are rare (see also Catcheside, 1938).

McClintock (1931) describes prophase configurations resulting from these abnormalities in *Zea*, and shows that the position of a gene may be identified by combined cytological and genetical work. For example, the **Blg** chromosome in a heterozygote lost 7% of its length from the short arm. This plant showed the **lg** character in place of the normal **Lg**. By X-raying seeds of hybrids heterozygous for **Plpl** and examining plants which were **pl** in type, McClintock found that the satellited chromosome had lost a portion of the long arm. In another plant, also with the **pl** character, a reciprocal translocation with another chromosome had occurred, accompanied by a deficiency at the point of interchange. This deletion included the locus of **Pl**. McClintock (1938) for example, shows that a ring-shaped chromosome carrying the factor $\mathbf{Bm}_1$ may be lost, or change in size during mitosis. When this chromosome is lost from cells containing both it and a normal chromosome bearing **bm**, or a deficiency of this locus, the tissues of the plant show the recessives characteristics. Therefore variegation for normal brown midrib is due, in this case, to the loss or change in size of the ring-chromosome. When the chromosome changes in size by abnormal division, McClintock noticed that the cells showed corresponding changes in type. Sectors which have either (1) colourless cell walls and no plastids, (2) colourless cell walls and colourless plastids (3) brown midrib cells, (4) pink tissues or (5) blotched chlorophyll pattern have been found together with compounds between them. McClintock suggests that these characters are due to losses of particular regions of the ring chromosome neighbouring on and including the locus of $\mathbf{Bm}_1$. McClintock (1931, 1933) has shown that multiple changes may be present together and that races of maize differ in respect of small inversions or deficiencies; but as McClintock remarks, the presence of a marker, such as a knob or centromere near the locus of a gene is necessary to localise that gene cytologically. Genetical means on the other hand lead quite frequently to precise localisation. The results of the experiments of McClintock (1930, 1931, 1932), Beadle (1932), Stadler (1931), Burnham (1930), illustrate the value of combined cytological and genetical work.

Stadler observed after X-raying that **C** and **sh** were often lost, unaccompanied by loss of **Wx**, but that the loss of **Wx** was always accompanied by loss of **C** and **sh**. The centromere is therefore presumed to be near **wx**. McClintock by studies of T8 – 9*a* has shown that the order is **C** – **sh** – **wx** – point of interchange in the short limb of chromosome 9 which has a sub-median centromere. Creighton and McClintock (1931) show by linkage studies that **C** is nearer to the knob at the end of chromosome 9 than **wx**. By crossing normal maize and reciprocal translocation T8 – 9 to *Teosinte* (*Euchlæna mexicana*), Beadle (1933) found that little or no crossing-over takes place in the **C-wx** interval. Cytological and genetical observation can therefore show that **wx** is near the centromere, that the point of interchange of T8 – 9*a* is in the long limb, and that the order and distances in cross-over units on the short limb of the chromosome are :—

knob, 20, **C**, 3, **sh**, 20, $\overset{\uparrow}{\mathbf{wx}}$, 8, $\mathbf{V}_1$, 4, point of translocation.

Although over forty genes are known in *Pisum sativum* it has been impossible to place these in the expected seven linkage groups in a satisfactory manner. The realisation of the presence of structurally changed lines on the one hand gives a reason for this fact and provides a means of more intensive analysis. The full analysis of structural changes in *Drosophila* by Bridges, Painter, Sturtevant, Dobzhansky, Beadle and Muller provides essential knowledge (see literature key).

ŒNOTHERA

Introduction. In 1886 de Vries (see de Vries, 1901) began an investigation of a population of *Œnothera Lamarckiana* which he discovered near Hilversum, in Holland. Since that time he has continued the investigations, while many other workers have been attracted to the work through the complex and novel problems which are encountered. It was found that some *Œnothera* species were not stable but on occasion gave rise to mutants, which might or might not remain stable. For example, de Vries found that *O. Lamarckiana* during eight generations of culture, gave rise to several new types, some of which had a moderately high frequency of recurrence (Table 46). Thus 53,509 offspring in one culture were true

Lamarckiana, while 350 were of the form called *oblonga,* 229 were *lata,* 158 were *nanella,* while other forms appeared in smaller numbers. Two important differences in behaviour from that of factor segregation should be noticed. First, it is found that the mutation rate is low (total about 1·5%) and is not amenable to interpretation on a basis of normal segregation; secondly, that the new forms differ from *Lamarckiana* by a complex of characters and thereby may again mutate to plants with characteristics quite definitely different from those of *Lamarckiana.*

It is not within the province of this book to review the whole literature of the subject, but rather to indicate the directions in which the investigations now in progress are proceeding.

The earlier workers were not aware of the methods now available for investigating such a problem as that of *Œnothera,* and the complicated results which were obtained during the breeding work were inexplicable.

It was thought by some that the behaviour of *Œnothera* was distinct from that of other more fully investigated species. The advent of cytological work on the species, however, facilitated the investigations, and since 1928 more and more workers have adopted the view that the behaviour of *Œnothera* is similar to, but much

TABLE 46

Pedigree of a Family of Œ. Lamarckiana (1886-99) (*Data of de Vries*)

Generation.	Gigas.	Albida.	Oblonga.	Rubrinervis.	Lamarckiana.	Nanella.	Lata.	Scintillans.
I					9			
II					15,000	5	5	
III				1	10,000	3	3	
IV	1	15	176	8	14,000	60	73	1
V		25	135	20	8,000	49	142	6
VI		11	29	3	1,800	9	5	1
VII			9		3,000	11		
VIII		5	1		1,700	21	1	
Total .	1	56	350	32	53,509	158	229	8

more complex than that of the ring forming diploid species already enumerated.

The genetic behaviour of species of *Œnothera*, which was studied first by de Vries and later by many other workers, appeared, until recently, to be anomalous in the plant and animal kingdoms. De Vries found that inbred *Œnothera Lamarckiana* produced in about 2% of cases several forms which were distinct in type. These sparse segregates he named *mutations* (formerly a generalised term), and supposed that they arose through some change in the immediately preceding cell generations.

Hybridisation between species was found to be comparatively easy and productive of peculiar and complicated results. Although several of the species bred true when selfed, crossing two species often gave rise to two or more distinct types of plants, and reciprocal crosses sometimes produced different results. For example, the cross, *O. Lamarckiana* × *O. Hookeri*, produces two forms, *læta* and *velutina* (de Vries, 1913). *Læta* is similar in reciprocal crosses but *velutina* is variegated if *Lamarckiana* is the female parent. *Læta* and *velutina* do not differ solely in one character but can be separated by a group of characters. The workers (see Renner (1914, 1917) and Honing (1911)) concluded that the twin hybrids produced in such a cross resulted from the fact that one parent (*Lamarckiana*) produced two types of gamete as in a heterozygote. Renner called the two *complexes*, which were found in the gametes of *O. Lamarckiana*, *gaudens* and *velans* respectively. When a *velans* gamete unites with the gamete of *Hookeri*, *velutina* results, while the union of gametes bearing *gaudens* and *Hookeri* give rise to *læta*. It is found that *O. Lamarckiana*, *biennis*, *muricata*, *suaveolens* and other similar species breed true when selfed, with the exception of a few mutations; yet they are heterozygous for two complexes. The reason why they breed true when selfed is furnished by the discovery of various anomalies in the physiology of the gametes and zygotes.

Seed Production. Seed production in selfed *O. Lamarckiana* is half that of *Lamarckiana* crossed with any other species of *Œnothera*, except *biennis* and some of its derivatives. Renner (1914) and Hiorth (1926) describe three types of fertilised ovules in selfed *O. Lamarckiana*. One half have normal embryos and endosperm and give rise again to *O. Lamarckiana*; they result from the fusion of gametes bearing the *velans* and *gaudens* complexes respectively. (It is useful to indicate the nature of the species in terms of complexes, thus—*velans-gaudens.*) One quarter of the ovules have small embryos and an empty endosperm sheath and consist of the *velans-velans* complexes, while another quarter have neither embryo nor endosperm: *gaudens-gaudens.* Hence it was realised that *O. Larmarckiana* bred true although heterozygous owing to the death, in the young stage, of the homozygote combinations. Meanwhile, Heribert-Nilsson (1912) found that a red-nerved race of *O. Lamarckiana* when selfed segregated in the ratio two red-nerved to one white-nerved (566**Rr** : 288**rr**) and pointed out that the **RR** zygotes were eliminated. De Vries was the first to suggest that homozygotic elimination was bound up with lethal factors in *Œnothera.*

Table 47 from Renner (1917) shows the seed production of various species of *Œnothera.* From it one sees that some species,

TABLE 47

Viable Seed Production of Œnothera Species

(After Renner, 1917)

100% represents a full viable seed production.

	Renner's observations.	de Vries' observations.
Lamarckiana, Her. Nilsson—red-nerved	23–33%	—
,, ,, ,, —white-nerved	30–49%	—
,, ,, ,, × *biennis*	46–55%	—
,, ,, ,, × *muricata*	91–98%	—
muricata	63–87%	91–97%
,, × *biennis*	—	95%
,, × *Lamarckiana*	48–80%	96%
suaveolens	15–46%	12–39%
,, × *biennis*	73–88%	93%
,, × *Lamarckiana*	91–93%	89–90%

which are known to produce twin hybrids on out-crossing, have a full seed production even when selfed. *O. muricata* is such a form. Elimination of gametes, instead of elimination of zygotes, takes place in this case, but both zygotic and gametic elimination may be found in one species. Whereas *O. Hookeri* has 100% good pollen and ovules, other species have a greater or less mortality of pollen or ovules (Davis (1910), Gates (1915), Geerts (1909), Renner (1914, 1917)).

Differential Lethality of Gametes. By various species crosses *O. muricata* was proved to produce two types of pollen (called *rigens* and *curvans*). Renner (1919*b*) identified the active *curvans* pollen as those grains carrying the smaller blunt-ended starch grains, as contrasted with the *rigens*-carrying pollen grains which have much longer spindle-shaped starch grains, and are non-functional or, as they are called, inactive. 50% pollen abortion can be observed in the pollen of *muricata* (see Fig. 46). Similarly, crossing experiments, using *muricata* as the female parent, show that only one type of ovule is functional, and that this type is different in genetic properties from the functional type of pollen. The active complex in the ovule is *rigens*, while the *curvans* complex inhibits embryo-sac formation. It should be noted for later remarks that in one and the same *muricata* plant, selection has been able to affect, independently and distinctly, the lethals governing egg and pollen. Renner (1921) found that in *O. muricata* any one of the four megaspores could give rise to the embryo-sac while in *O. Hookeri* and *O. Lamarckiana* it was mainly the one at the micropylar end of the row of four megaspores which functioned. This so-called *Renner effect*, which has also been reported in *O. nutans* and *O. pycnocarpa* (Atkinson, (1916, 1917) and Ishikawa (1918)) would account for the fact that only *rigens* megaspores function on the female side of *O. muricata*. Four megaspores result from the two divisions of meiosis, therefore *rigens* will separate to the two megaspores at the chalazal end, and *curvans* to those at the micropylar end or *vice versâ*.

Observation shows that in *O. muricata* the embryo-sac may be formed in the normal position (the micropylar end) or at the chalazal end. It is found that in both cases the embryo-sac contains the *rigens* complex. The interpretation of this is that, when the *curvans* complex is carried by the micropylar megaspore the *rigens* megaspore at the chalazal end competes with it. Since *curvans* contains lethals only functional in embryo-sac formation, the megaspore at the chalazal end containing the *rigens* complex forms the embryo sac. This is confirmed by the figures in which it can be seen that (1) when only the megaspore at the micropylar end forms an embryo-sac no other megaspore develops further, (2) when megaspores at the chalazal end form embryo-sacs the megaspore at the micropylar end is swollen but not functional. *O. muricata* therefore has differential gametic elimination and when selfed produces a full seed production of *rigens-curvans* zygotes (Fig. 45).

An interesting example of gametic elimination is seen in the cross *suaveolens* × *muricata*, where one of the hybrid types results from the union of the *curvans* complex from *muricata*, with *flavens* from *suaveolens*. In this hybrid two pairs of factors, **B** for large leaf *vs.* **b** for small leaf, and **M** for margined leaf *vs.* **m** for not margined leaf are arranged **Bm** *flavens*, **bM** *curvans*. The hybrid (*flavicurva*) produces pollen carrying all the possible combinations of factors and complexes, with the exception of **Bm** *flavens* but embryo-sacs of this constitution may be formed. This shows that the complex **Bm** *flavens* is viable in the pollen of the parent *suaveolens*, but that it is inviable in the pollen of the hybrid.

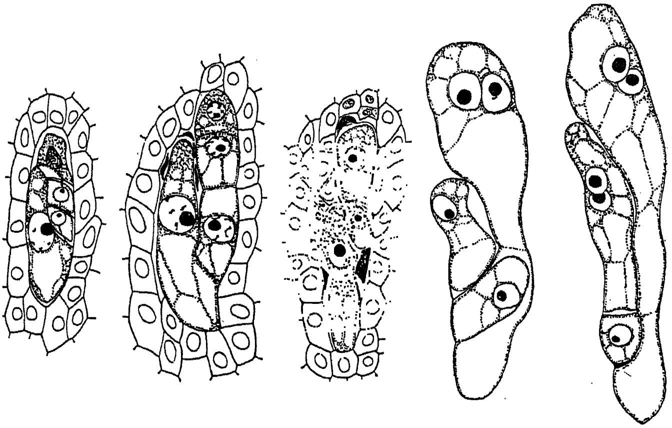


FIG. 45. Embryo-sac development in *Œnothera muricata*. Competition between the megaspores at the chalazal end and those at the micropylar end in the formation of the embryo-sac. In other ovules only the megaspore at the micropylar end (the uppermost cell) develops as in *O. Hookeri* (normal). (Renner, 1921.)

In the *rigens-velans* hybrid resulting from the cross *muricata* × *Lamarckiana* the factors **Str** *vs.* **str** segregate. It is found that there is only 25% active pollen and that only the combination Str and *velans, i.e.,* the paternal complex, is active.

Certation. In passing, it should be mentioned that de Vries (1913), Renner (1914, 1917, 1921*a*), Davis (1926), Heribert-Nilsson (1925) and Hiorth (1926), show that there are several places in the life cycle where certation between the gametes or zygotes bearing different complexes can be observed. For example, de Vries found that *læta* and *velutina* sometimes appeared from the cross, *Hookeri* × *Lamarckiana* not in the ratio 1 : 1, but ranged from the extremes 7% *læta* to 68% *læta.* Renner (1919*a,b*) and Hiorth (1926) found that if a small amount of pollen is used, *læta* appears in 22%—42%, but with normal pollination there is 9%—17% *læta.* Both pollen germination and pollen tube growth of *gaudens*-carrying pollen (giving *læta* with *Hookeri*^{h}) is less than that of *velans* pollen (giving *velutina* with *Hookeri*^{h}). Heribert-Nilsson had found that pollen of *Lamarckiana* which carried the factor R for red nerves grew faster than pollen carrying r for white nerves. Hiorth further analysed this and other cases.

	læta.	*velutina.*
Hookeri × *Lamarckiana*, white-nerved (rr)—		
sparse pollination	40	56
normal	30	148
Hookeri × *Lamarckiana*, red-nerved (Rr)—		
sparse pollination	34	111
normal	31	248

It will be noticed that in the second group of crosses the proportion of *velutina* is greatly increased.

	R *velutina* (red nerves).	r *velutina* (white) nerves).	*Læta.*
Hookeri × *Lamarckiana* red-nerved (Rr) totals—			
sparse pollination	127	125	90
normal pollination	336	228	744

The above results indicate that *velans* pollen bearing the factor r grows faster than *gaudens* but more slowly than *velans* bearing the factor R. There is a difference in the rates of growth of *gaudens*

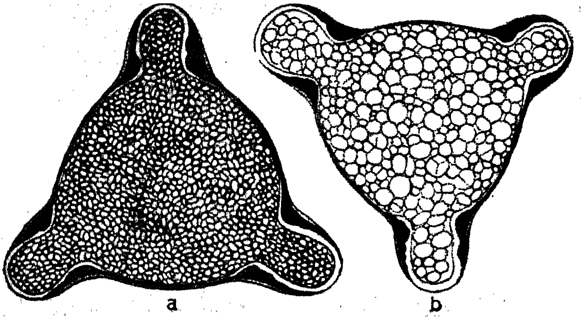


FIG. 46. Pollen grains of *Œnothera muricata*, *a*, active *curvans*, *b*, inactive *rigens*. (Renner, 1919.)

pollen bearing the **R** and **r** factors respectively, but this is not so noticeable as in the case of *velans*. With sparse pollination the *læta* plants segregated 36 **Rr** to 54 **rr**. By separating the zygotes from the top and bottom halves of the ovary Hiorth found that in sparse pollination r *gaudens* fertilised almost all the eggs in the upper half of the fruit. These pollen tubes reach the ovule more quickly than pollen tubes bearing the other three genetic contents. Contrary to the above relationships between **R** and **r** *velans*, it is found that **R** decreases the growth rate of *gaudens* as compared with r.

In the hybrid *velans-curvans* resulting from the cross *O. Lamarckiana* × *muricata* the pollen-grains bearing *curvans* can be distinguished from those bearing *velans* by their types of starch grains (see Fig. 45). It has been observed that the *curvans* type does not grow as fast as the *velans*. Using pollen from the hybrid on the short-styled flower of *O. muricata* a number of *curvans* pollen tubes reach the ovule, but using the same pollen on the longer-styled flower of *O. Lamarckiana* only the *velans*-bearing pollen tubes reach the ovules.

Davis has shown that the pollen tubes from *O. brevistylis*, which is a derivative of *O. Lamarckiana*, grow more slowly than those bearing the normal *velans* or *gaudens* complexes. Species of *Œnothera*, therefore, exhibit to an extreme degree, gametic and zygotic elimination and certation. It is only in the last ten years that a plausible theory for the origin of these phenomena has been made.

THE FACTOR COMPLEX THEORY

Renner (1917, 1919*a*, *b*, 1921*a*) put forward the factor complex theory which has been accepted by almost all workers in the field of *Œnothera*. It is indeed more than a theory, since it is a statement of fact. The heterozygous species of *Œnothera* produce two types of gametes that are apparently distinct and which differ in a number of closely coupled factors. The stability of the complex throughout many generations is at present exceptional among plants or animals. It should be pointed out that the " factors " which constitute the distinctive effect of the complex upon the phenotype are probably mendelian factors, but generally there is no means of isolating them, since their allelomorphs cannot be identified.

Certain examples are instructive in showing that the constancy of these complexes depends on a mechanism which has become highly specialised in *Œnothera* by the action of natural selection. For the recognition of the complex, Renner gave names to the gametic complements of the *Œnothera* species. Below are given a few of these complexes in well-known species of *Œnothera*, together with an indication as to whether they are functional on the female or male side or on both.

	functioning in egg.	*functioning in pollen.*
O. Lamarckiana	*velans-gaudens*	*velans-gaudens*
O. biennis	*albicans-(rubens)*	*(albicans)-rubens*
O. suaveolens	*flavens-albicans*	*(albicans)-flavens*
O. muricata	*rigens-(curvans)*	*curvans-(rigens)*
O. cruciata	*pingens-(flectens)*	*(pingens)-flectens*
O. strigosa	*deprimens-(stringens)*	*stringens-(deprimens)*

The complexes in brackets are inviable.

It will be noticed in the above list that *O. biennis* and *O. suaveolens* have the complex *albicans* in common, and it has been found that the complexes *rubens* and *gaudens* are very similar in character. The occurrence of the same complex in two or more species has been

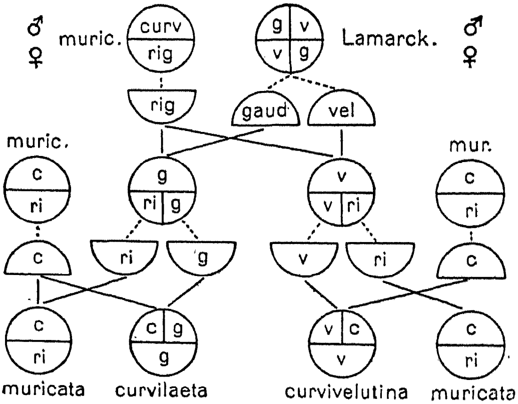


FIG. 47.—Scheme of the reciprocal crosses between *Œnothera muricata* and *O. Lamarckiana* and of the back cross of *O. rigidilaeta* and of *O. rigidivelutina* to *O. muricata* ♂. (Renner, 1929.)

reported in numerous cases. It has also been found that almost all species of *Œnothera* can be hybridised, giving fertile F_1s if the genom is not antagonistic to the plasma. A diagrammatic explanation of the reciprocal crosses between *muricata* and *Lamarckiana* is given in Fig. 47.

The above complexes have been recognised by the behaviour of the species in several species hybrids. The following diagram illustrates the behaviour, due to gametic elimination, of the reciprocal crosses between *muricata* and *biennis*.

	biennis female	*muricata* male	*muricata* female	*biennis* male
gametes	*albicans*	*curvans*	*rigens*	*rubens*
F1 zygotes	*albicurva*		*rubirigida*	

	albicurva female	*rubirigida* male	*rubirigida* female	*albicurva* male
gametes	*albicans*	*rubens*	*rigens*	*curvans*
zygotes	*biennis*		*muricata*	

The F_1s of the reciprocal crosses differ in a considerable number of characters and may be regarded as two new distinct types. On selfing they do not segregate for *biennis* or *muricata* characters, but breed true for a considerable number of their characters. When however, the two F_1s are again intercrossed reciprocally, the original species *biennis* and *muricata* are recovered.

The products of a particular cross can be postulated on the basis of experience gained from the use of the parental species in other crosses. Thus it is known that *Lamarckiana* produces two types of gametes, *velans* and *gaudens* on both male and female sides and that *suaveolens* produces functional *albicans* and *flavens* in the egg while only *flavens* is functional in the pollen. In the cross, *suaveolens* × *Lamarckiana* four types are therefore expected in the progeny :

velans — albicans, (1) *albivelutina*

velans — flavens, (2) *flavivelutina*

gaudens — albicans, (3) *albilæta*

gaudens — flavens, (4) *flavilæta*

The cross *biennis* × *Lamarckiana* gives *albivelutina* and *albilæta* as in the previous cross. The reciprocal cross *Lamarckiana* × *biennis* only gives *rubivelutina* (also known as *fallax*). The expected type resulting from the fusion of *gaudens* and *rubens* is inviable. Renner (1917)showed that the zygote in the presence of the r factor only reached the stage where there were one or two cells in the embryo and a diseased endosperm, a behaviour comparable in fact to the homozygote (*gaudens-gaudens*).

Both types (*gaudens-rubens* and *gaudens-gaudens*) in the presence of **R** may develop a many-celled embryo before death. Other work indicates that *rubens* and *gaudens* complexes are similar.

It has been pointed out that the heterozygous species of *Œnothera* behave as if they consisted of two gametic complexes. These complexes cannot exist as such in the homozygous state without some change in the genetic properties of the complex. It was realised by the earlier workers that the differences between the complexes of one species must be controlled by many factors. There was little reason to believe that the factors in one complex were necessarily allelomorphic to those in the opposing complex. Some workers suggested that the factors of one complex were close to one another on one chromosome and therefore rarely, if ever, crossed over. We shall see later that chromosomal linkage (catenation) and not genetic linkage is the real explanation of the general non-segregation of the component factors which differentiate one complex from another.

Lethal Factors. To account for the non-survival of homozygotes and for the inviability of gametes Davis (1915), de Vries (1917), Muller (1917, 1930*a*,*b*), Morgan (1919), Shull (1923), *et al.* suggested that lethal factors were present.

Heribert-Nilsson (1912) found that on selfing *O. Lamarckiana* segregation of the allelomorphic factors **R** for red nerves *vs.* **r** for white nerves was 2 : 1 in place of 3 : 1. Renner (1914) also found that only 50% of the embryos in *O. Lamarckiana* were sound and suggested that the formula for the heterozygous red-nerved plants was **RrLl**, while that for the recessive white-nerved plants was **rrLl** : all embryos containing **RR** or **LL** or **ll** die. With this hypothesis only the plants of the constitutions **RrLl** and **rrLl** survive out of the 16 genotypes in a dihybrid segregation from selfing. The ratio of **RrLl** to **rrLl** is of course 4 : 2. Hence in this heterozygote **Rr**, the ratio of normal to lethal embryos is 6 : 10, which approximates to the 1 : 2 ratio found by de Vries (1913), while the white-nerved individuals will have 50% inviable embryos through the lethality of **LL** and **ll**. Renner (1925) points out that **L** and **l** should not be considered to be genes, but that they represent the sum total of the genotypic constitution of each complex in one respect. (Renner supposed that besides the factors which segregated normally there were others which controlled the definite characteristics of the complex.) They are representatives of Renner's "rest." In passing, it should be mentioned that generally all the mendelian factors which are included in the first linkage group of *Œnothera*, behave in segregation as if closely linked to lethals of the complex. Catcheside (1937) has shown from his work on trisomics that the balance and unbalance as visualised by Bridges rather than definite lethal factors are involved in the preservation of the heterozygosity of such forms as *O. Lamarckiana*.

Balanced Lethal Mechanism. Muller (1917), in a paper on an *Œnothera*-like case in *Drosophila* and again in 1928 and 1930*a*, put forward the theory of balanced lethals to account for the puzzling phenomena in *Œnothera*. The homozygote Beaded wing in *Drosophila melanogaster* is a dominant lethal, and hence the ratio obtained in crossing two heterozygotes is usually, 2 Beaded : 1 normal-winged individuals. By artificial selection Muller isolated a strain which bred nearly true for Beaded wing, with the exceptional occurrence of a normal fly. Nevertheless the constant Beaded wing line was heterozygous for Beaded, since it gave a 1 : 1 ratio on crossing to normal (see p. 66). Muller found that the constancy of the Beaded strain was due to the appearance of a lethal factor **l** on the third chromosome which carried the normal allelomorph to Beaded at a locus close to Beaded. The constitution of the strain of flies was therefore $\frac{\mathbf{Bd\ L}}{\mathbf{bd\ l}}$, which, when bred from would give three classes of flies, homozygous **Bd L** and homozygous normal **bdl**, both of which would die, and the third class similar to the heterozygous parents. The rare occurrence of a cross-over between the loci **Bd** and **L** would give normal flies without the lethal factor. In this experiment Muller also found that a suppressor of crossing-over was present. This of course would further aid the true breeding potentialities of the heterozygous strain. Similar cases in

Drosphila, Antirrhinum and maize have since been reported by other workers (see p. 64).

Under the influence of a balanced lethal mechanism any true factor mutation would be preserved in the heterozygous condition and thus free from any effect of natural selection towards its elimination. Therefore, once established, the balanced lethal mechanism would favour the accumulation of recessive factors in a latent condition. Any mutations which favoured the support of the balanced lethal mechanism, such as suppressors of crossing-over, also would be favoured. Hence new characteristics would be formed by factor mutation in one complex and not in the opposing complex. The appearance of a rare segregate or mutant of de Vries was thus thought to be due to the occasional crossing-over between the balanced lethals and a particular character determiner. This, and the foregoing hypothesis, were put forward on orthodox grounds without a suspicion that the behaviour of the chromosomes of *Œnothera* was dissimilar to that of other plants. Muller supposed that the lethals were linked to the factors controlling the special complex differences between one chromosome and its homologue.

Œnothera Lamarckiana gives rise to the form *nanella* in about 0·3% of cases during eight generations of selfing (de Vries). This *nanella* form appears to be governed by a single factor difference from normal *Lamarckiana*. A factor **n** for dwarfness is carried by the *gaudens* complex, but it is not normally present in the *velans* complex, therefore all *Lamarckiana* plants are heterozygous **Nn** and tall, since the homozygotes *gaudens* and *velans* are both lethal. If a rare cross-over takes place between the *gaudens* and *velans* complex in such a way that the recessive factor **n** is transferred to *velans* the mutant *nanella* would appear through the fertilisation of the *velans* gamete (called *nanovelans*) by a *gaudens* gamete containing **n**. When this mutant *nanella* (*gaudens-nanovelans*) is crossed to other species it may or may not segregate. The reasons for non-segregation are (1) the opposing complex in the new hybrid contains no recessive factor **n** and (2) the *nanovelans* complex enters into a new-balanced lethal system with the different complex.

For example, *O. biennis* × *O. Lamarckiana nanella* gives the hybrid (*albicans-nanovelans*), which is tall and does not segregate on selfing. But the cross *Lamarckiana* × *biennis* (*rubens-nanovelans*) is dwarf and is homozygous for n (*rubens* is similar in constitution to *gaudens*). From the cross *muricata* × *Lamarckiana nanella* the F_1 (*rigens-nanovelans*) is tall and segregates in the F_2. This is possibly due to the fact that in *rigens-nanovelans* crossing-over may take place more easily between the balanced lethals and *nanella* than in *albicans-nanovelans*.

De Vries (1913, 1918) and Shull (1923) showed that the alternative characters, yellow and sulphur flower colour, were allelomorphic in *suaveolans* and *biennis* (S s). When the cross S female × s male was made the F_1 was yellow (S). The reciprocal cross was sulphur (s).

The F_2 did not segregate but, like the F_1, was the colour of the male parent. The suggestion is made that S for yellow is linked to an egg lethal and s for sulphur is linked to a pollen lethal. Therefore functional eggs only carry s and functional pollen only carry S. Shull obtained cross-overs between these factors and the lethals, and therefore obtained plants in which the colour followed the opposite parent, and he also obtained them free from lethals. In this latter case the inheritance was normal.

Catenation. Gates (1908) first called attention to the fact that the chromosomes of *Œnothera* had a tendency to remain in groups of more than two chromosomes at the reduction division. Later Cleland (1922, 1923, 1925), Emerson (1924), Oehlkers (1926), Håkansson (1926) and others showed the correlation between the heterozygous species of *Œnothera* and ring formation of the chromosomes. As a result of much painstaking work between 1922 and 1928 it was discovered that there was a definite arrangement of the chromosomes in the ring which could consist of an even number of from four to fourteen chromosomes, with the remainder as bivalents. Sometimes two or more small rings were formed instead of bivalents (see p. 287). It was found that different hybrids had different but constant (with few, but important, exceptions) numbers of chromosomes in the ring and that those hybrids with large rings had more of the mendelian factors linked to one another than the hybrids with smaller rings of chromosomes.

It was thought that the maternally and paternally derived chromosomes alternated in the ring at the reduction division so that paternal chromosomes went to one pole and maternal to the other. The telosynaptic hypothesis, now replaced by the parasynaptic hypothesis, aided this interpretation to a small extent, but it hindered the standpoint now adopted that besides having an alternate arrangement in the ring the paternally and maternally derived chromosomes have a definite position in relation to each other.

If all the paternal chromosomes in the ring went to one pole and all the maternal chromosomes to the other, the complexes contained in each set would not be mixed and would remain as entities as long as the ring mechanism continued unchanged. Cleland and Oehlkers (1929) mention 20 species hybrids in which (1) the hybrids varied greatly in the number of chromosomes in the ring as compared with the parents, (2) two factors showed different linkage relationships in different hybrids, (3) where a ring consisted of a large number of chromosomes, segregation was at a minimum, but where few chromosomes were involved in the ring there was clear-cut segregation. *Cf.* Oehlkers (1926), Rudloff (1929), Gerhard (1929) and Hoeppener and Renner (1928).

Structural Hybridity. The reader will at once observe that these facts in *Œnothera* are similar in kind, but of more extreme degree, to those described earlier (see p. 252) in *Datura, Pisum, Zea, Campanula* and other plants of structural hybrid nature. Darlington (1929*a*, 1931*b*), Cleland and Blakeslee (1930), Håkansson (1929*b*) and Muller (1930), Catcheside (1932, 1933, 1938) have adopted the structural hybridity theory for *Œnothera* with far-reaching results.

The main points of the theory will be discussed below, but a much fuller contribution is made by Darlington (1931*b*) in a masterly and condensed treatise.

There are three main phenomena in *Œnothera* which should be associated together, (1) balanced lethal mechanism, (2) ring formation, (3) association of many genetical factors into one linkage group.

In species with ordinary pairing resulting in bivalents, the presence of a single balanced lethal system, such as is supposed to exist in *Œnothera*, can control one linkage group, *i.e.*, the factors carried by one pair of chromosomes at most. Further, it reduces the fertility of the plant by one half. If the heterozygosity of such a species is to be preserved in respect of all the chromosomes by a balanced lethal mechanism the fertility would be $\frac{1}{2}^{7}$, a negligible quantity. Suppose that a balanced lethal mechanism existed on one pair of chromosomes and segmental interchange took place between that pair and a non-homologous pair; the mechanism would then control four chromosomes in place of two without further reducing the fertility. Naturally, any increase in the number of chromosomes in the ring following hybridisation or by internal interchange followed by selfing, would be favoured by natural selection. Renner (1927), Darlington (1929*a*).

A species forming bivalents of the constitution, *AB AB, CD CD, EF EF, GH GH, KL KL, MN MN, OP OP*, can, by six interchanges between non-homologous chromosomes, give rise to a type with a ring of fourteen chromosomes, *AB BC CD DE EF FG GH HK KL LM MN NO OP PA*. Such a type would give rise to gametes containing paternally or maternally derived chromosomes, namely, *AB CD EF GH KL MN OP* and *BC DE FG HK LM NO PA*, *i.e.*, two complexes.

It will be seen that in the ring of fourteen, one chromosome is homologous at opposite ends with ends of two different chromosomes; thus the *C* segment of *BC* is homologous with the *C* segment of *CD* and the *B* segment with the *B* segment of *AB*.

Differential Segment. The cytological findings (Darlington, 1931*b*) show that chiasma formation takes place between homologous segments and hence crossing-over may occur between factors placed on the terminal segments of these chromosomes. Factors in these segments may thus pass from one complex to another. Pairing is usually restricted to the ends of the chromosomes and it is possible that the middle portion is not homologous with any part of either of the adjacent chromosomes. In any case, crossing-over does not seem to occur normally in the middle part of the chromosomes.

Various genetical and cytological data indicate that the middle portion is of appreciable size and Darlington suggests that the causes underlying the differences in properties of opposing complexes together with the so-called balanced lethal mechanism lie in this region of the chromosomes. Each chromosome therefore consists of two terminal segments which pair with terminal segments of two other chromosomes and one median differential segment which is supposed to contain the factors controlling the balanced lethal mechanism and the differences between the complexes.

The differential segments could be formed through segmental interchange in the following manner. In the original bivalent-forming line *AB CD* two parts of the *B* segment can be represented as *X* and B_1, *X* representing the inner portion of the *B* segment, *i.e.*,

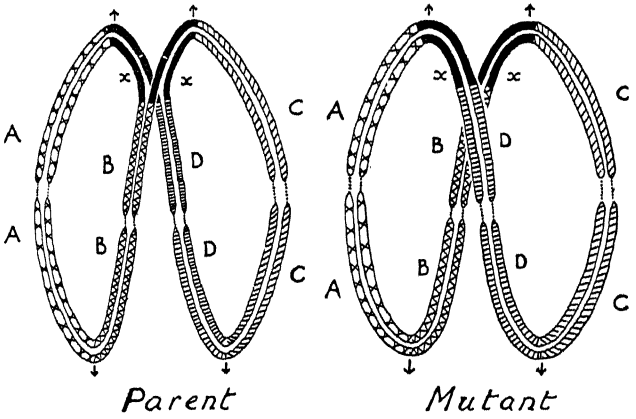


FIG. 48. Diagram showing the origin of a "lethal" system, "complex" system, and ring formation by crossing-over between translocated and non-translocated interstitial segments "*x*." The parent structural hybrid plant of constitution *AB, AxB, CD, CxD* gives a mutant with a ring of four of the constitution *AB, DxC, CD, DxA*. The only viable gametes that can be produced by such a system are (i.) deficient in *x*, and (ii.) reduplicated in *x*. They differ in segmental constitution and, meeting, will produce the "mutant" structural hybrid with a ring of four. The points of crossing-over in the *x* segments of two chromatids in the parent are marked by a gap. Terminalisation has taken place and been arrested by the change of homology. (Darlington, 1931*b*).

the line is *AXB*1 *CD*, etc. By translocation the portion *X* may be transferred to the *CD* chromosome (*CXD*), and a different line, *AB*, *CXD*, will be created. The hybrid between these two lines will be of the constitution, *AXB CD CXD AB*. Fig. 48 shows the configuration that would arise if a chiasma were formed in the *X* segments in such a hybrid.

Segmental Interchange. Somewhat similar configurations have actually been observed in *Œnothera* by Darlington (1931) and in *Pisum* by Sansome, E.R. (1932). (See Fig. 17.) These have been

considered on p. 84. Chiasma formation in the *X* segment will produce the crossed-over chromatids *AXD* and *BXC*. A gamete containing *AXD* and *BXC* on uniting with a gamete from the ancestral line *AB CD* will give a form having a ring in which the middle portions of the chromosomes are distinct *AB*\ /*CD*\
\BXC/ \DXA.

If reduplication or deficiency of the *X* segment does not cause gametic inviability a condition may arise in which only zygotes of the constitution *AXD BXC AB CD* are functional. In other words the balanced lethal mechanism may be constituted not by factors but by the balance of factors contained in the differential middle segments. Thus homozygotes (*AXD BXC AXD BXD*) and (*AB CD AB CD*) may be non-functional through the two-fold reduplication or deficiency of the *X* segment.

Renner's " Rest." That the contents of the differential segments, or, in genetical terms, the " Rest " of Renner are diverse, is indicated by the fact that some heterozygotes such as *biennis*, do not give viable homozygotes, while others such as *Lamarckiana* may give rise, as the result of interchange, to normal homozygotes such as *deserens*, *blandina*, etc. Others, again, such as the heterozygote of the complexes (*truncans-gaudens*) give rise to crippled plants, which are presumably homozygotes (Cleland and Oehlkers, 1929).

The hybrid from *suaveolens* × *biennis* produces a functional homozygote (*flavens—flavens*) known as *lutescens* (Renner, 1927) through crossing-over between *flavens* and a complex with which it is not usually in association, namely *rubens*. This homozygote has seven pairs of chromosomes.

Renner (1921*b*) had suggested that where one complex, such as *curvans* in *muricata*, is more viable in the pollen, any greater success of the other complex in the embryo-sac production will be favoured by the greater fertility of the plant. Since the distinctive features of the two complexes are suggested to be in the differential segments which do not form chiasmata, and which from the foregoing discussion presumably will differ quantitatively and qualitatively in their genetical material, it can be seen that the action of natural selection on the materials in one differential segment does not interfere with that of another. Hence the separation of the differential segments from the pairing segments allows new factors to arise independently for each complex through natural selection. It is therefore possible to have widespread interspecific hybridisation in the genus *Œnothera,* since the ends of the chromosomes are homologous throughout the group while the middle segments may not be.

It can be seen therefore that the view sometimes held, that a species hybrid is characterised by an anomalous behaviour compared with that of the parent species, is erroneous. In *Œnothera,* two heterozygous species may give rise through hybridisation to a homozygous seven bivalent " hybrid " which is similar in its genetical behaviour to the many non-ring-forming plants that have been studied. It will be realised that the homozygous derivatives of a ring-forming heterozygote might show chiasma formation in the middle segments as well as the end segments of the chromosomes. But in derivatives of hybrids such as (*flavens-subcurvans*), Rudloff (1929) or of the half-mutant forms such as *rubrinervis,* which arises from *Lamarckiana* and gives rise to the homozygous mutant *deserens,* it would be expected that differentiation would be negligible, since the mutant homozygote would have the direct descendants of the chromosomes of one complex in the heterozygote. (In the hybrids between *suaveolens* and *strigosa* (*flavens-strigens*) and between *purpurata* and *suaveolens* (*flavens-purpurata*^{h}) which have seven pairs of chromosomes, one might find that the middle segments had differentiated from the common ancestral type.)

It should be possible to study the amount of differentiation of the middle segments of the complex that has taken place during isolation from the time that it was contributed in its ancestral form to both of the heterozygotes.

The second class of mutation arising through the rearrangement of the genetical material illustrates the complicated phenomena to be expected in a ring-forming diploid organism.

CROSSING-OVER IN THE MIDDLE SEGMENTS

Darlington (1931*b*) and Sansome, E. R. (1932) have observed figure-of-eight configurations of chromosomes in *Œnothera* and *Pisum* respectively. This figure-of-eight configuration arises through the formation of a chiasma in a middle segment, the *X* segment, of two otherwise non-homologous chromosomes in a ring. This middle segment has different homologies from the end segments as postulated earlier (see Fig. 48, p. 280).

Let us consider a ring of six chromosomes in *Pisum* which arose from crossing two plants each of which gave a ring of four chromosomes when crossed to normal. There must be a chromosome in common in the two rings. Thus the rings of four can be represented as *AB* \ *BC* / *CD* \ *DXA* and *EF* \ *FD* / *DC* \ *CXE*.

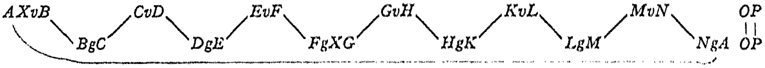
Interchanges in the normal line *AB CD EF GH*, etc., could have taken place between *CD* and *AB* on the one hand, and *CD* and *EF* on the other hand to give the other two lines. The *X* segment may have been formed as a result of these interchanges having taken place at different levels on the *CD* chromosome. If we divide the *D* segment into four portions, 1, 2, 3, 4, with 1 nearest the *C* segment and call the *CD* chromosome *C*1, 2, 3, 4, then one interchange between *AB* and *C*1, 2, 3, 4 may result in *e.g* *A*1, 2, 3, 4, and *BC*, while the other interchange between *EF* and *C*1, 2, 3, 4 may be, *e.g.*, *F*3, 4 and *C*1, 2, *E*. Representing the segments 1, 2 by *X* and 3, 4 by *D*, we obtain *AXD BC* and *FD CXE*. On crossing these two plants with rings of four chromosomes, four possible types can be obtained in the ratio, one normal line : two lines with a ring of four corresponding to the original rings of four : 1 line with a ring of six. This ring of six is arranged thus :—

AB \   / *CXE* \   / *FD* \   *GH*   *KL*   etc.
                            | | | |
\ *BC* /   \ *EF* /   \ *DXA*   *GH*   *KL*   etc.

in which the top line represents the gametic complement derived from one parent and the lower line that derived from the other.

In a certain proportion of cases, depending upon the position and size of the *X* segment relative to the other segments, a chiasma is formed between the *X* segments in chromosomes *AXD* and *CXE*. This gives rise to the figure-of-eight configuration which is important in several respects. On studying the chromatids involved in the chiasma at the *X* segment it is seen that two correspond to the original chromosomes *AXD* and *CXE*, while *two are constituted by CXD and AXE* (see Fig. 48).

For our present purpose, it is necessary only to consider the consequences of such a figure-of-eight configuration in a ring-forming species of *Œnothera* such as *Lamarckiana*. *Œnothera Lamarckiana* gives rise to many forms, the origin of many of which can be explained by the above theories. The ring of twelve chromosomes and one bivalent of *O. Lamarckiana* can be represented by :—



v and *g* represent the differential segments which presumably carry the characteristics of the complexes *velans* and *gaudens* respectively together with the so-called lethals (the origin of the *v* segment is unknown) while the two *X's* represent two homologous median segments in different chromosomes.

Origin of Half-Mutants. By crossing-over in the *X* segment four different chromatids involving the *X* segment will be obtained, namely *AXvB GXvB GXgF AXgF*. Segregation of these chromatids (with a numerically even number of chromosomes) will be non-disjunctional for two of the four and disjunctional for the other two according to the orientation of the ring. In the diagram (Fig. 48) the two crossed-over-chromatids will disjoin regularly, while the original chromatids will show non-disjunction at one end. Hence with this method of disjunction the resulting gametes with the new types will probably be viable and those with the original types inviable.

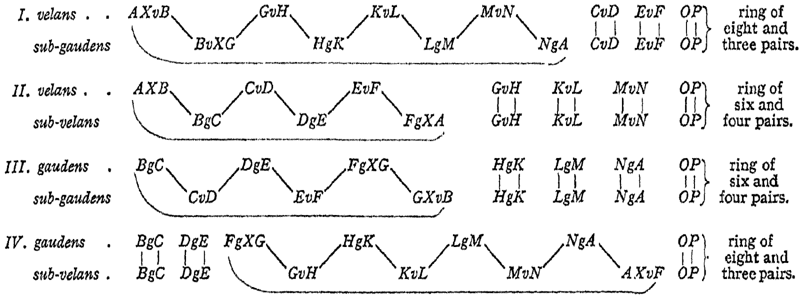
The original gametic complements of *O. Lamarckiana* were :—

velans .	*AXvB*	*CvD*	*EvF*	*GvH*	*KvL*	*MvN*	*OP*
gaudens .	*BgC*	*DgE*	*FgXG*	*HgK*	*LgM*	*NgA*	*OP*

After crossing-over in the *X* segment and regular disjunction for the crossed-over chromatids there results :—

sub gaudens	*GXvB*	*CvD*	*EvF*	*AgN*	*MgL*	*KgH*	*OP*
sub velans .	*BgC*	*DgE*	*FgXA*	*NvM*	*LvK*	*HvG*	*OP*

These gametic complements on meeting unchanged *gaudens* or *velans* will give rise to four different heterozygotes with different chromosome configurations.


I. velans . .
sub-gaudens
AXvB BvXG GvH HgK KvL LgM MvN NgA
CvD CvD EvF EvF OP OP
ring of eight and three pairs.
II. velans . .
sub-velans
AXB BgC CvD DgE EvF FgXA
GvH GvH KvL KvL MvN MvN OP OP
ring of six and four pairs.
III. gaudens .
sub-gaudens
BgC CvD DgE EvF FgXG GXvB
HgK HgK LgM LgM NgA NgA OP OP
ring of six and four pairs.
IV. gaudens .
sub-velans .
BgC BgC DgE DgE
FgXG GvH HgK KvL LgM MvN NgA AXvF
OP OP
ring of eight and three pairs.

For example, *O. Lamarckiana* with a ring of twelve and one pair of chromosomes produces *O. rubrinervis* with a ring of six and four pairs in about 0·1% of the progeny (Cleland, 1925). *O. rubrinervis* is a so-called half-mutant since it produces the fertile mutant *deserens* in ¼ of the seed. The remaining ¾ of the seed is made up of ½ *O. rubrinervis* and ¼ inviable embryos (de Vries (1918), Cleland (1925)).

The complexes of *O. rubrinervis* can be represented as *sub-velans-pænevelans*. Renner (1927) concluded from genetical analysis that *sub-velans* arose through crossing-over between *velans* and *gaudens*, since it exhibited qualities of both, while Hoeppener and Renner (1928) suggested that *pænevelans* and *velans* did not differ greatly when combined with other complexes (except with *sub-velans*). The second of the formulæ given above (*velans-sub-velans*) agrees well with the description of *O. rubrinervis*, while *subvelans-subvelans* would give a form with seven bivalents in which the differential segments of *gaudens* and *velans* have been recombined. This form corresponds to *deserens*. The form *velans-velans* will constitute the inviable embryos while half the seed will again reproduce *O. rubrinervis*.

The half-mutants, *erythrina*, *blandina*, *rubrisepala* probably arose in a similar fashion, either as the result of crossing-over between the same differential segments or between those of other chromosomes. *Erythrina* gives rise to the segregating factor for fragilis. This is expected if the factor for fragilis is carried on the *X* or differential segments which become homozygous, and pair in a similar way to the terminal segments. In the formula above it will be seen that the segments *Xv* of chromosomes *AXvB* and *BvXG* are continuations of pairing segments whereas in the ancestral *velans-gaudens* arrangement they are isolated from one another.

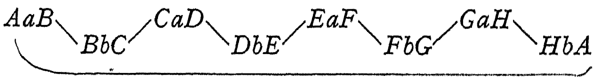
The above theory of the origin of half-mutants and secondary full mutants predicts that in (1) the frequency of occurrence of the half-mutant should be constant, since it is a function of crossing-over between definite lengths of chromosomes.

(2) The particular mutant at every appearance should have the same characteristics.

(3) The complexes of the mutant should be unchanged and consist of a mixture of the parental complexes.

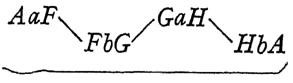
(4) One "half and half" complex survives as a homozygote, such as *subvelans-subvelans,* while the other dies, *subgaudens-subgaudens.* Through crossing-over, the lethal factors of *velans* have been transferred to the *gaudens* complex, giving rise to viable *subvelans* and lethal *subgaudens.* In a trisomic form, one chromosome is left free to pair with any other homologous part, therefore exceptional crossing-over may take place more frequently. It follows therefore that half-mutants will be produced more frequently and in greater variety in the trisomic forms than in a diploid.

Mass Mutants. Interchanges between segments within one complex also would give rise to mutant forms. A probable case is that in which the segments *B* and *F* in a ring of eight,

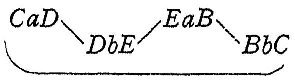


$$\underbrace{AaB \diagdown BbC \diagup CaD \diagdown DbE \diagup EaF \diagdown FbG \diagup GaH \diagdown HbA}$$

interchange to give a viable gamete with one new type of arrangement which with the complementary complex will give



$$\underbrace{AaF \diagdown FbG \diagup GaH \diagdown HbA}$$



$$\underbrace{CaD \diagdown DbE \diagup EaB \diagdown BbC}$$

i.e., the new form will have unchanged physiological properties but the pairing properties will be changed (two rings of four and three bivalents) ; the new form will be indistinguishable from the old but naturally the range in gametic output is increased. The chromosomes of one ring will disjoin independently from that of the other, therefore there are four possible gametic types. The sudden appearance of several new forms, though possible in the immediate progeny of this plant, is more likely to occur in later generations.

Discussion. On the above theory of the origin of ring forming species of *Œnothera,* together with the necessary assumption of specificity of pairing, one is able to explain the known facts of behaviour and to make predictions of the configurations of chromosomes to be found in hybrids between two known species.

Analysis and prediction have been made by Cleland and Blakeslee (1930), Cleland (1931), Catcheside (1932–1938) and Darlington (1931*b*).

The following table of configurations of several species has been adapted from Darlington (1937) :—

TABLE 48

Summary of Ring-forming Properties in forms of Œnothera *

1. SPECIES.

Species.	Complex Constitution.	Configuration.
Heterozygotes :—		
Œ. grandiflora	acuens.truncans	(14)
Cockerelli	curtans.elongans	(14)
strigosa	deprimens.stringens	(14)
muricata	curvans.rigens	(14)
suaveolens	flavens.albicans.	(12) + (2)
Lamarckiana	velans.gaudens.	(12) + (2)
biennis	rubens.albicans	(8) + (6)
Homozygotes :		
Œ. franciscana	^{h}franciscana.^{h}franciscana	7 (2)
Hookeri	^{h}Hookeri.^{h}Hookeri	7 (2)
purpurata	$_h$purpurata.^{h}purpurata	7 (2)
2. HYBRIDS BETWEEN HETEROZYGOTES.		
Heterozygotes :		
Œ. Lamarckiana × *strigosa.* (and reciprocally)	(i) velans.stringens	(6) + (4) + 2 (2)
	(ii) gaudens.stringens	(14)
	(iii) deprimens.velans	(10) + 2 (2)
	(iv) deprimens.gaudens	(10) + 2 (2)
Œ. Lamarckiana × *suaveolens.* (and reciprocally)	(1) velans.flavens	2 (4) + 3 (2)
	(ii) gaudens.flavens	(12) + (2)
	(iii) albicans.velans	(14)
	(iv) albicans.gaudens.	(8) + (6)
Œ. suaveolens + *strigosa.*	(i) flavens.stringens	(4) + 5 (2)
	(ii) albicans.stringens	(12) + (2)
	(iii) deprimens—flavens	(12) + (2)
	(iv) albicans.deprimens	(not obtained)

* From D (1931*d*), Catcheside (1933), Cleland (1935). (*Reproduced by kind permission from Darlington (1937)*).

TABLE 48—*continued*

3. HYBRIDS BETWEEN HOMOZYGOTES AND HETEROZYGOTES.		
Heterozygotes :		
Œ. *muricata* × *Hookeri.*	rigens.^{h}Hookeri	(6) + 4 (2)
Œ. *Hookeri* × *muricata.*	^{h}Hookeri.curvans	(6) + (8)
4. HYBRIDS BETWEEN HOMOZYGOTES.		
Heterozygotes :		
Œ. *deserens* × *blandina.*	subvelans.^{h}blandina	(6) + 4 (2)
Œ. *deserens* × *purpurata.*	subvelans.^{h}purpurata	(4) + 5 (2)
Œ. *blandina* × *purpurata.*	^{h}blandina.^{h}purpurata	(4) + 5 (2)
5. DERIVATIVES OF HYBRIDS.		
Œ. *lutescens* (ex *suaveolens* × *biennis*).	$^{\text{let.}}$flavens.^{x}flavens	7 (2)
Œ. *suaveolens* ×	—	
pachycarpa. F_1	—	(6) + (4) + 2 (2)
,, F_2	—	(6) + 4 (2)
6. MUTANTS.		
Œ. *rubrinervis* (ex *Lamarckiana*).	subvelans.pænevelans	(6) + 4 (2)
Œ. *deserens* (ex *rubrinervis*).	subvelans.subvelans	7 (2)
Œ. *ochracea* (ex *grandiflora*).	acuens.acuens	7 (2)

Cleland (1931) brings out one consequence of the theory, namely, that those complexes which are genetically closely related yield either bivalents or small rings, when combined with each other, while those with greater differences give larger rings in the hybrids. Hoeppener and Renner (1928) constructed a diagram of the relationships which they found between various complexes on purely genetical grounds. Cleland (1931) superimposed on this diagram (see Fig. 49), the configurations known to be produced in the complex combinations. He found that the distances between the complexes on Hoeppener and Rennner's diagram corresponded to the size of the ring in the zygote produced by the combination of the complexes. Only a slight alteration was required to make the cytological and genetical diagrams agree entirely, namely, that *rigens* be placed as in the diagram further from *velans* and that the position of *velans* and *Hookeri*^{h} be reversed. It has already been mentioned that *rubens* and *gaudens* are very similar genetically. It has been found that both give similar configurations when combined with every other complex so far studied. *Hookeri*^{h} and *velans* are not identical but closely related genetically and give related configurations, *e.g. gaudens-velans* (12) and (2) ; *gaudens-Hookeri*^{h} (10) and 2(2) : *albicans-velans* (14) ; *albicans-Hookeri*^{h} (14) ; *flavens-velans* (4) and (4) and 3 (2) ; *flavens-Hookeri*^{h} (4) and 5 (2), Cleland (1931).

The reason for the above phenomena is not difficult to understand.

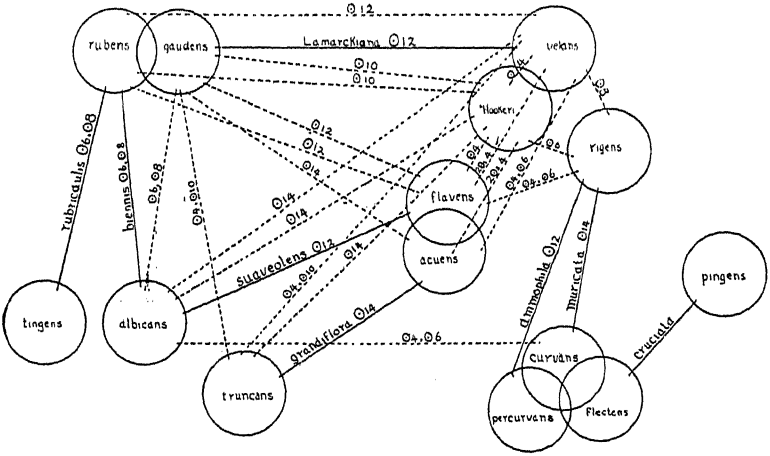


FIG. 49. Modification of Hœppener and Renner's diagram showing the genetic relationships between certain complexes of *Œnothera* together with the chromosome configurations produced by the various complex combinations. Solid lines connect complexes associated in spontaneous races. Dotted lines connect complexes associated in artificial hybrids. (Cleland, 1931.)

Closely related complexes probably arose by the same or similar segmental interchanges. By continued isolation in different heterozygotes (such as *rubens* in *biennis* and *gaudens* in *Lamarckiana*) there is opportunity for factor mutations to occur. This does not disturb the pairing properties of the end segments. If the requirements of natural selection have been met in a heterozygous species with a large ring, or two large rings, the products of any segmental interchange between non-homologous segments will not be spread through the population.

Two out of many interesting examples illustrate the possibilities and behaviour of *Œnothera*.

When *O. Chicagœnsis* (*excellens-punctulans*) is crossed with *O. biennis* (*rubens-albicans*) the normal hybrid is *rubens-excellens*. Occasionally, however, *punctulans-rubens* appears in a small proportion of the progeny. When the latter is crossed with *biennis* as female, one of the possible types is *albicans-rubens* or *biennis*. Cleland (1931) reports that this resynthesised species has a ring of six and a ring of eight typical of the original *biennis*.

Gates and Catcheside (1931) intercrossed the homozygous mutants *O. deserens*, *O. purpurata* and *O. blandina*. Each has seven pairs of chromosomes. The cross, *deserens* × *purpurata* gave a ring of four and five pairs, *blandina* × *purpurata* a ring of four and five pairs, *deserens* × *blandina* a ring of six and four pairs.

A start has been made in mapping the chromosomes of *Œnothera* and describing the interchanges that have taken place to form the various complexes. Cleland and Blakeslee (1930), Cleland (1931) and Emerson and Sturtevant (1931) have compared the configurations formed in different combinations of the complexes and come to a definite conclusion as to the chromosomes involved.

The following is a list compiled from these authors in which we have adopted lettering for the segments of the chromosomes in place of the numbers which these authors have used. The arbitrary normal line is *Hookeri*^{h} with chromosomes therefore labelled *AB CD EF GH KL MN OP*.

Hookeri^h	*AB CD EF GH KL MN OP*
flavens	*AD BC EF GH KL MN OP*
velans	*AB CD EH GF KL MN OP*
excellens	*AB CD EF GL HK MN OP*
strigens	*AD BC EL GH KF MN OP*
gaudens	*AB CP EF GD NL MH OK*
rubens	
albicans	*AD CE FH GL KN MP OB* or *AD GP*, etc., Emerson and Sturtevant.
franciscans	*AB CD EF GL HK MN OP*
sub-velans	*NM EH FG DL CP OK*
sub-gaudens	*MH FE GD NC PO KL*

In conclusion, the adoption of the theory of segmental interchange for the origin of ring-forming plants and of the theory of specificity of pairing has revolutionised the views and lines of work on *Œnothera* and other species. All the consequences of the two theories have not been mentioned in this short summary, but it is hoped that it will indicate the trend of thought of cytogeneticists. One consequence, however, should be mentioned. The number of chromosomes allotted to each gamete depends on regular disjunction occurring at the heterotype division. The mechanism of disjunction of rings is of a particular and complicated type, and is expected to produce irregularities more frequently than that governing bivalent separation. Therefore, as expected, we find that polyploid and aneuploid forms are noticeably frequent in *Œnothera*. The gametic output of any heterozygous form of *Œnothera* with more than 14 chromosomes will obviously be varied since the presence of reduplicated segments will influence the manner of ring formation and of disjunction. It is therefore not surprising that there are many more primary trisomics than the seven expected types (see p. 295). Attempts were made by the earlier workers to apply the complexes of a diploid *Œnothera* to the polyploid derivative. For example, the *Lamarckiana gigas* 4*x* and *semigigas* 3*x* mutants were supposed to be made up of *gaudens* and *velans*. There were two *gaudens* and two *velans* in *Lamarckiana gigas* and a proportion of two to one in *semigigas*. It was soon found, however, that the complexes lost their identity at the first meiosis of the new form. This is to be expected on cytological grounds, since the configuration of chromosomes will no longer be a ring of twelve and one pair as in the diploid, or two rings of twelve and two pairs as expected in the tetraploid. The physiological properties of the gametes produced by trisomics and aneuploids of *Œnothera* are different from those of organisms which are not structural hybrids, since the variety of the output is large and involves reduplication and deficiencies of differential as well as of pairing segments. Therefore in *Œnothera*, as distinct from most other plants, zygotes with chromosome numbers ranging from 14 almost continuously to 28, 29 and 30 are functional.

Reference should be made to Gates (1928), who has done a considerable amount of work on these forms and to Lehmann (1922) for further information on polyploid *Œnothera*.

LINKAGE BETWEEN GENETIC FACTORS

Renner (1925), etc., and Shull (1923, 1928*b*, 1929, 1930) came to the conclusion that there were three or four recognisable linkage groups among the *Œnothera* species. Shull enumerates the factors in each group thus: linkage group 1, **M m** margined *vs.* non-margined leaf, **N n** normal *vs.* nanella habit, **S s** yellow *vs.* sulphur flowers and **P p** punctate *vs.* non-punctate stems (nomenclature of Emerson and Sturtevant, 1931). There has been so far no crossing-over between the factor for *rubricalyx* buds and punctuate stems, therefore the latter authors provisionally made the following allelomorphic series founded on Renner's original factor **P**.

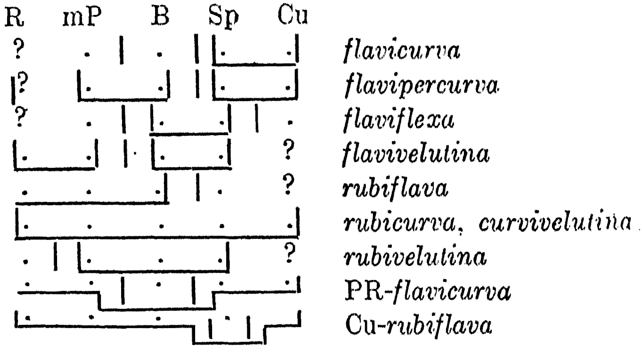


FIG. 50. Linkages of factors in different *Œnothera* hybrids. Horizontal lines indicate linkage and vertical lines separate factors which are independent. (Renner, 1928.)

Pr (the **Rh** factor of Shull) red hypanthium.
Ps (**PStr** of Renner, **Rc** of Shull) *rubricalyx.*
P (**Pstr** of Renner) striped buds, punctate stem.
p (**r** of Shull) green buds.

Linkage group 2 includes only the factor for *brevistylis.*

Linkage group 3 consists of **V v** normal *vs.* old gold flower colour, **Bu bu** normal *vs.* bullate leaf and a factor for doubleness. All these factors are stongly linked to one another. Cleland and Brittingham (1934) point out that the genes of linkage groups 1 and 3 which are supposed to be on the ring of twelve chromosomes in *Œnothera*

Lamarckiana segregate in different proportions from the heterozygote. Obviously both *velans* and *gaudens* must contain the recessive allelomorph before the character appears in the progeny Therefore crossing-over from one complex to the other must occur·

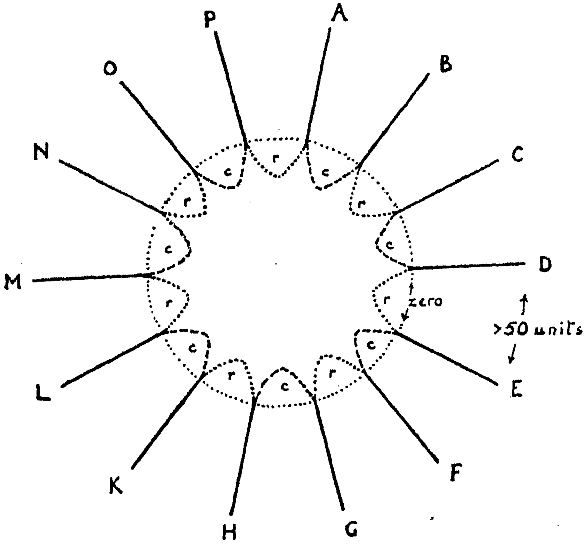


FIG. 51. Diagram to represent potential crossing-over map in *Œnothera muricata* of the constitution.

curvans : A_cB C_cD E_cF G_cH K_cL M_cN O_cP
rigens : B_rC D_rE F_rG H_rK L_rM N_rO P_rA

c represents the differential middle segments of the seven *curvans* chromosomes, *r* those of the *rigens* chromosomes. Crossing-over occurs between terminal segments with the same capital letters, not between the *c* and *r* segments adjacent to these. The lengths of the interior segments are shown equal and likewise those of the exterior segments, but this is arbitrary, for their lengths must be variable following the occurrence of segmental interchange as a result of exceptional crossing-over within the circle, *i.e.*, between complex differentials. *Note :* This map corresponds to a constant complex, not to changes of complex with which most crossing-over determination in *Œnothera* are concerned. (Darlington, 1931*b*.)

The amount of crossing-over between the points of interchange and the gene can therefore be roughly indicated by the proportion of recessives given by a heterozygous *O. Lamarckiana.* Linkage group 3 consisting of 3 closely linked genes is situated on a chromosome of the ring of 12 sufficiently far from the point of interchange to show independence with the linkage group 1, whose genes may show chromosome linkage with one another and with the complex.

Shull worked with only a limited range of material, including *Lamarckiana*, *biennis* and their derivatives, and Renner points out that in other material the factors of linkage group 1 may be independent of one another. Renner (1928) gives as an example the following diagram of linkages between five factors : **R** for red nerves, **Pm** for margined leaf, **B** for broad leaf, **Sp** for pointed leaf, and **Cu** for pendulous tip Fig. 50. It will be seen that in *rubicurva*, and *curvivelutina* all five factors are linked to one another, but in *flavicurva* m and **B** are independent from one another and from the linked factors **Sp** and **Cu**.

Renner (1928), Cleland and Oehlkers (1930), Emerson (1930, 1931*a*,*b*), Emerson and Sturtevant (1931), and Sturtevant (1931) realised that the linkage phenomena were due to ring formation. This is, in general, similar to that already discussed in *Pisum*, maize and *Campanula*. But, as Darlington (1931*b*) pointed out, the linkage map of an *Œnothera* species should be represented as follows (Fig. 51), since the differential middle segments do not normally cross over.

Emerson and Sturtevant (1931), Renner and Cleland (1933) identify the following segments of the chromosomes composing the complements of the species enumerated above with the genes :—

R in 1·2	(*AB*).
P in 3·4	(*CD*).
Tr in 1 or 4	(*A* or *D*).
pusilla in 1·4	(*A* or *D*).
s in 0·3	(*C*).
N in 3 or 4	(*C* or *D*).
V in 5 or 6	(*E* or *F*).
sp in 5·6	(*GH*).

The following experiments of Emerson (1930, 1931*a*,*b*) illustrate well the type of phenomena to be expected in *Œnothera* and the lines along which future work requires to be done.

Œnothera franciscana has 5 bivalents and a ring of four, Cleland (1922), and is genetically homozygous and free from lethals. It contains the dominant factor (S) for flower colour and recessive (gr) for green bud cones and the dominant normal tall habit (**D**). After crossing *O. franciscana* with *O. biennis* a form *franciscans-sulphurens* arises with green bud cones (**Gr**) and sulphur flowers (**s**) which is otherwise similar to *franciscana* in habit. This form has 50% abortion of pollen and a ring of twelve and one pair (Cleland, 1923), or a ring of ten and two pairs (Emerson, 1931*a,b*).

Franciscans-sulphurens, when inbred, segregates a form, sulphur dwarf, in 3% of the progeny. Sulphur dwarf differs in size and colour of bud cones (**d gr**), has no gametic lethals and has seven pairs of chromosomes.

Segregation of **S** : **s** in the F_1 between *franciscana* and *sulphurens-franciscana* back-crossed to *sulphurens-franciscana* is

	S	s
Eggs	2,133	821
Pollen . . .	370	180

In both cases there is a deficiency of the recessive form. On the other hand, the dwarf habit of sulphur dwarf segregates in a 3 : 1 ratio without deficiency. The factor for green cones **Gr, gr,** is linked to a pollen lethal, hence in the F_1 of *franciscana* with **gr** × *sulphurens-franciscana* **Gr** there were found 537 **gr** : 0 **Gr.**, and in the reciprocal cross 269 **gr** : 248 **Gr** indicating that *franciscana-sulphurea* was heterozygous, **Gr gr.** The constitution of *O. franciscana* is *franciscans-franciscans*, of *O. franciscana-sulphurea* is *sulphurens-sd-franciscans*, and of sulphur dwarf is *sd-franciscans-sd-franciscans.*

The factors **Spl** for splashed bud cones and **d** for dwarf are almost completely linked in *sulphurens-sd-franciscans*, while in *sulphurens-franciscans* the factors **Spl gr** and **s** are closely associated (**Spl–gr** 3·5% **gr–s** 4·5%). Hence it is probable that **s** and **d** are independent. The first two hybrids have rings and the last hybrid has seven pairs of chromosomes. Emerson points out that if these factors are in separate chromosomes which participate in the ring in *sulphurens-franciscans* they will show linkage with one another but not in a form with seven pairs of chromosomes.

Trisomics. Catcheside (1932, 1936), Emerson, S (1935) have shown that there are many more trisomics in *Œnothera* possible than the 7 primary trisomics expected on the chromosome number. By non-disjunction in the ring of twelve of *O. Lamarckiana*, 8 chromosome gametes may be produced. The gametes will contain a *velans* or a *gaudens* complex combined with any one of the 7 *velans* or *gaudens* chromosomes. If a trisomic (*velans-gaudens* + 1) is formed by this type of gamete it will give rise again to *O. Lamarckiana* and further trisomics. Such trisomics, of which 13 are expected, are *O. scintillans*, *O. lata* and *O. cana*. If an extra chromosome of the *gaudens* complex counteracted the lethal effect of *velans-velans*, we expect 12 more trisomics, which will breed true since the zygotes without the extra chromosome will be inviable.

Double non-disjunction on the same side in the ring of twelve whereby non-disjunction takes place at two places in the ring will give rise to 48 different trisomics. Therefore 73 trisomics are theoretically possible of which 60 are monomorphic, *i.e.*, breed true. About 10 monomorphic trisomics are known.

CHAPTER X

INTERSPECIFIC HYBRIDISATION

Galeopsis—Triticum—Nicotiana—Crepsis—Viola.

THE results of the investigations in different genera by geneticists, cytologists and taxonomists will be summarised in this chapter.

A cursory outline of the genetics of interspecific hybrids will be made in such a way that the new outlook on the species question may be understood. It will also be seen that much monographic work on genera is essential for the understanding of many biological problems of the future.

Galeopsis. Müntzing (1930*a,b,* 1932*a,b*) crossed *Galeopsis pubescens* ($2n = 16$) with *G. speciosa* ($2n = 16$). A partially sterile diploid hybrid gave 200 plants in the F_2. One of these F_2 plants was triploid and was somewhat similar in appearance to the *G. Tetrahit* occurring in nature. This triploid was crossed with *G. pubescens* and gave one seedling—a tetraploid ($2n = 32$). The tetraploid was perfectly fertile and in all respects similar to the wild *G. Tetrahit*. The artificial *G. Tetrahit* crosses readily with natural *G. Tetrahit* and gives rise to fertile hybrids.

The meiosis of the hybrids between the artificial and wild *G. Tetrahit* shows a preponderance of bivalents, indicating that the chromosomes carried in the tetraploid derived from *pubescens* and from *speciosa* are homologous in part at least with the chromosomes of *G. Tetrahit.* The facts that pairing takes place between the chromosomes of *speciosa* and *pubescens* in the diploid F_1 hybrid and that trivalents are present in the triploid and tetraploid hybrids, indicate that the chromosomes of *speciosa* and *pubescens* have parts in common. Müntzing has gathered together a large amount of material on the subject of sterility in *G. Tetrahit,* and in hybrids with another tetraploid species *G. bifida,* which is presumed to be of analogous or similar origin to *G. Tetrahit.* He is of the opinion that sterility may be explained on a basis of two factors.

We pointed out (1932) that it seemed possible that the sterility was due to inter-homology between chromosomes of two or more of the ultimate parental species. Müntzing supposed that the chromosomal constitution of the artificial *G. Tetrahit* is **pr**/**ps** where **p** and **s** represent pubescens and speciosa chromosomes, and **r** a set of recombination products between **p** and **s**.

Müntzing (1938) shows that wild races have 95% of fertile pollen when inbred, but the hybrids have varying amounts of sterility and show occasional bivalent and polyvalent formation. He suggests that both sterility and meiotic irregularities are due to structural differences between the lines.

Triticum. The considerable work that has been done on the *Secale-Triticum-Ægilops* group discloses an interrelationship between the sets of chromosomes of the polyploids. The wheats are divided into diploid, tetraploid and hexaploid varieties ($x = 7$), while *Ægilops* species are diploid or tetraploid.

Wheats

Einkorn Group $n = 7$.	Emmer Group $n = 14$.	Vulgare Group $n = 21$.
T. ægilopoides.	*T. dicoccoides.*	*T. Spelta.*
T. thaoudar.	*T. dicoccum.*	*T. vulgare.*
T. monococcum.	*T. durum.*	*T. compactum.*
	T. turgidum.	*T. sphærococcum.*
	T. pyramidale.	
	T. polonicum.	
	T. persicum.	
	T. timopheevi.	

Hybrids of diploid ($2n = 14$) with tetraploid ($2n = 28$) or hexaploid ($2n = 42$) wheats are almost entirely sterile, but hybrids between tetraploids (the *Emmer* group) and hexaploids (the *vulgare* group) are comparatively fertile. F_1 pentaploid hybrids form 14 bivalents and 7 univalents at meiosis. The bivalents disjoin normally while the univalents split longitudinally at the first division and pass at random to opposite poles at the second division. Occasionally laggard univalents appear and are not included in the daughter cells. The gametes therefore contain, in general, $14 + 0$ to 7 chromosomes. In agreement with this, Kihara (1919, 1921, 1924), Sax (1923) and Watkins (1924) found F_2 plants with chromosome numbers ranging from 28 to 42.

Kihara (1921, 1924) and Watkins (1924) found that all of the expected zygotic series were not obtained and that the F_2 could be divided into two classes—the "diminishing group" and the "increasing group." The diminishing group consisted of plants containing from 28 to 34 chromosomes which normally formed 14 bivalents and 0 to 6 univalents. (The plants having 35 chromosomes formed 14 bivalents and 7 univalents like the F_1 plants.) The increasing group consisted of plants containing 36 or more chromosomes and the sum of the number of bivalents and univalents equalled 21. The above plants were normal in vigour and more or less fertile, hence Kihara termed them fertile combinations.

Occasionally dwarf and sterile plants occurred which contained more than 35 chromosomes. The manner in which the chromosomes paired, however, did not conform with that of the "increasing group," *e.g.*, 20 bivalents, or 15 bivalents and 4 univalents were formed. Kihara called these plants sterile combinations.

Kihara (1921, 1924) and Watkins (1924, 1925, 1927*a,b*) found that on selfing plants of the diminishing group the progeny consisted of plants containing the same number of chromosomes as the parent or a lower number. In later generations 28 chromosome plants were obtained. Similar breeding work with plants of the increasing group gave plants with the same number or a greater number of chromosomes than the parent, and eventually plants with 42 chromosomes were obtained.

The haploid complement of the tetraploid Emmer group is generally believed to be homologous with 14 of the 21 chromosomes of the vulgare group. The *AB* sets of the Emmer are combined in *vulgare* wheats with a group *D*, possibly from an *Ægilops* species such as *A. cylindrica.* Variations in the number of bivalents found in the pentaploid hybrids and partial sterility in crosses within the Emmer group have shown that differentiation within the sets of chromosomes has occurred since the formation of the varieties. Lilienfeld and Kihara (1934), for example, found that the hybrids of *T. timopheevi* with other tetraploid varieties contain quadrivalents, trivalents, bivalents and univalents. Since *T. timopheevi* crossed with the diploid wheat *T. ægilopoides* forms bivalents and univalents as expected, the authors show that *T. timopheevi* contains the *A* set common to both diploids and tetraploids and a *G* set which has probably been differentiated from the more usual *B* set by methods seen in the previous chapter. The occurrence of two rings of four chromosomes in *A. speltoides* × *T. monococcum* is in agreement with this hypothesis. By intensive study Kihara and Lilienfeld have shown that there are four semi-homologous *C* sets among the *Ægilops* species and that these are related distantly to the *A* sets of *Triticum* and to *S*, *T*, *E*, *F* and *D* sets of *Ægilops*. The nomenclature of the sets would seem advantageous for practical reference, but it is important to notice that phytogenetical relationship can be traced between the *A* set and the *D* set of wheat and that the *B* set of *T. durum* bears some relationship to both *A* and *G*. Therefore specific origin should not be implied in the use of this terminology.

Pentaploid wheat hybrids are difficult to analyse genetically since most of the characters segregate in a complex manner. Moreover, there is great variability in many of the characters. Often, indeed, they exceed the limits set by the parental forms and new characters and abnormal types also appear. In the progeny of these hybrids, association of certain characters (types) is common and there has been a tendency to study the inheritance of types rather than single characters.

Watkins (1927*a*) obtained similar results to Kihara (1924) and concluded that there was a definite relation between type and chromosome number. Crosses between F_1 (*turgidum-vulgare*) and *vulgare* gave :—

(1) Plants with more than 35 chromosomes which were of *vulgare* type and bred true for this type.

(2) Plants like the F_1 with 35 chromosomes and which gave *vulgare* and *turgidum* types in the progeny.

Crosses between F_1 (*turgidum-vulgare*) and *turgidum* gave :—

(1) Mostly plants of *turgidum* type which bred true for this type.

(2) A few plants having 35 chromosomes.

After studying thirteen pairs of alternative characters, Thompson (1925) was able to group the F_2 into three classes. He concluded that certain characters were associated and association was found to be greatest between those characters which were generally characteristic of the species.

From an economic point of view it is desirable that certain characters should be transferred from one group to the other, *e.g.*, the rust resistant character of the forms with 28 chromosomes to the forms with 42 chromosomes.

Some characters are easily transferred from one group to the other but other characters are seldom transferred. Watkins (1927*b*) (*turgidum* × *vulgare*) found that the characters keeled *vs.* round glumes were easily transferred and had no association with chromosome number. The transferring of the rust resistant character, Sax and Gaines (1924) consider as difficult but not impossible. Tochinai and Kihara (1927) found that in the F_4 of a cross, rust resistant (28 chromosomes) × susceptible (42 chromosomes) the plants with 28 or 29 chromosomes were resistant in a variable degree while all the plants with 42 chromosomes were susceptible. They concluded, therefore, that this character was associated with chromosome number. Other morphological characters were also considered to be associated with chromosome number, *e.g.*, plants of the increasing group never had pithy straw. Similar results with regard to rust resistance were obtained by Hayes, Parker and Kurtzweil (1920), Thompson (1925), Aamodt (1927) and Stevenson (1930).

Occasionally an exceptional resistant *vulgare* type was obtained, Thompson (1925) and Stevenson (1930). Thompson found three plants of *vulgare* type which were somewhat less resistant than the *durum* parent. A few other characters may behave in this way, *e.g.*, solid *vs.* hollow straw. Thompson (1925) and Watkins (1927*a*).

Sax (1923) (*durum* × *vulgare*) also found a correlation between five characters and chromosome number. He therefore concluded that the 7 unpaired *vulgare* chromosomes carried the factors for the distinguishing character of the *vulgare* wheats. Thompson (1925) and L. A. Sapehin (1928), however, consider that this conclusion is unjustified. Tochinai and Kihara also suggested that these 7 chromosomes carried the factors which weaken the resistance to rust. On this basis the rare transference of a character may be explained by assuming that one of the 7 chromosomes occasionally pairs with an *Emmer* chromosome.

Watkins (1927*b*) has attempted to make an exact factorial analysis of *turgidum* × *vulgare*.

The parents of the F_1 possessed the character waxy foliage and the F_1 plants were also waxy.

The F_2 consisted of waxy and non-waxy plants, the latter being of the *turgidum* type.

The F_1 ♀ × *turgidum* gave all waxy plants, half of which bred true for waxy, while half gave waxy and non-waxy. The F_1 was therefore heterozygous for the factors **W** (waxy) and **w** (waxless).

The F_1 ♀ × *vulgare* gave only waxy plants which bred true for waxy. The unpaired *vulgare* chromosomes were therefore considered to have introduced an extra factor for waxy $\mathbf{W}^1$.

Watkins explains these results by assuming that the *turgidum* parent has the formula (**WW**), and the *vulgare* parent (**ww**)$\mathbf{W}^1\mathbf{W}^1$. The factors in the brackets are supposed to be carried by the chromosomes which pair and segregate normally in the hybrid. The factor $\mathbf{W}^1$ is supposed to be carried by one of the *vulgare* chromosomes which are unpaired in the hybrid. He has shown that half of the hybrids (*turgidum* × *vulgare*) × *vulgare* give a few waxless sterile combinations. Thus zygotes (**ww**)$\mathbf{W}^1$ having more than 35 chromosomes would give a few waxless sterile combinations, since they would contain some of the 7 *vulgare* chromosomes which were unpaired in the F_1, represented twice as bivalents. The plants therefore would not contain representatives of all the 7 unpaired *vulgare* chromosomes and would lack at least the chromosome carrying $\mathbf{W}^1$. A few (**ww**)$\mathbf{W}^1$ or (**Ww**)$\mathbf{W}^1$ plants having 35 chromosomes, however, would occur. These would give some waxless fertile combinations having less than 35 chromosomes, *i.e.*, *turgidum*-like. Such types were observed by Watkins and Cory (1931).

Good 1 : 1 ratios were obtained by Watkins and Cory in a study of the following characters in the progeny of the F_1 back-crossed with the parental species: rough *vs.* smooth chaff, red *vs.* white chaff, waxy *vs.* waxless foliage, beardless *vs.* bearded ears, and keeled *vs.* round glumes. Linkage was observed between the factors for keeled and bearded. This behaviour indicates that allosyndetic pairing is the rule. If the $\mathbf{W}^1$ chromosome paired with the **w** chromosome and the **W** chromosome remained unpaired (autosyndesis) a 1 : 1 ratio would also be obtained. Such pairing is unlikely, since the parental forms are frequently recovered in the

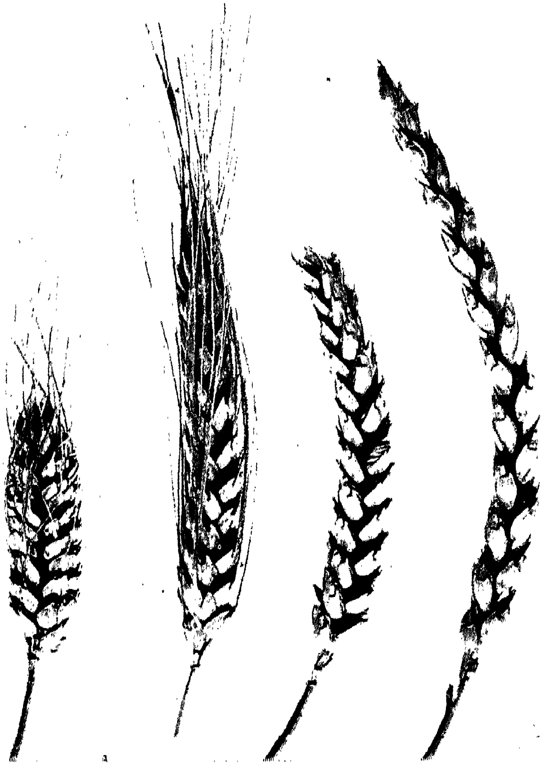


FIG. 52. Ears of: *a*, round-glumed *turgidum* = 28 chromosome **kk.** Extracted type. *b*, keeled *turgidum*, parent variety = 28 chromosome **KK.** *c*, round *vulgare*, parent variety = 42 chromosome **kk.** *d*, keeled *vulgare*, the type speltoid = 42 chromosome **KK.** Extracted type. (Watkins, 1927.)

back-cross. This evidence also suggests that 11 or 12 of the chromosomes of the two species are closely similar. It should be noted

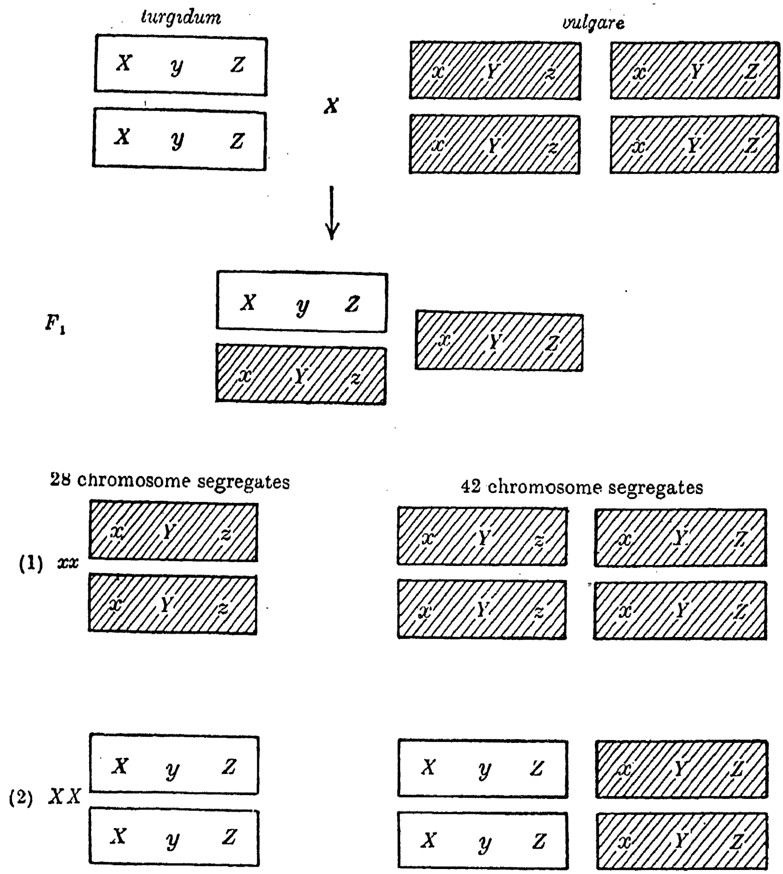


FIG. 53. Diagram of the association of type with chromosome number. The character determined by *X* is transferable from one species to another. The type is associated with chromosome number, since the 42 and 28 chromosome segregates will differ by *Z* if both are *xx*, and by *Y* if both are *XX* (*vulgare* chromosomes shaded). (Watkins, 1930.)

that Watkins has more recently suggested a similar explanation for the chromosome relationships in interspecific *Nicotiana* hybrids.

Watkins and Cory point out that all 28 and 42 chromosome wheats are not expected to have the above formulæ, *e.g.*, *T. spelta* var. White spelt is either $(WW)W^1W^1$ or $(WW)w^1w^1$.

Waxless is a new character which occurred in the F_2 and was associated with low chromosome number in accordance with the above hypothesis.

As already mentioned, Watkins found that the characters keeled and round glumes were not associated with chromosome number and were easily transferred from one species to another. He also found that other characters were transferred to *vulgare* together with keeled glumes thus producing the speltoid—a special type associated with high chromosome number.

The *turgidum* parent had keeled glumes of normal thickness and a moderately dense ear. These characters he regards (1928) as being due to a group of completely linked factors represented by K. The *vulgare* parent had round glumes of normal thickness and a moderately dense ear—k. K is supposed to produce the keel to the glume and to increase the thickness of the glume and the laxity of the ear. k represents the group of recessive allelomorphs to those of the K group.

On crossing the two species 28 KK and 42 kk, two new types also associated with chromosome number were obtained, (1) 42 KK, the *speltoid* type: this is a *vulgare* type having a lax ear and thick keeled glumes which are only pulled away from the grain with difficulty, (2) 28 kk, a *turgidum* type: this has a very dense ear and thin rounded glumes. This interpretation is supported by evidence from crosses between speltoid, *vulgare*, *turgidum* and the F_1 (*turgidum-vulgare*) Fig. 52.

Comparison of the two round-glumed types—*turgidum* 28 kk and *vulgare* 42 kk—showed that they differed in other characters. The same applied to the two keeled glume types, *turgidum* 28 KK and speltoid 42 KK. Watkins therefore considers that the unpaired *vulgare* chromosomes have an effect like K and suggests that one of them carries a group of linked factors K^1. The formulæ given to the parents is therefore (KK) for *turgidum* and $(kk)K^1K^1$ for *vulgare*.

Out of the apparent chaos in segregation of these pentaploid hybrids Watkins has isolated certain main features—single pairs of characters are often associated with chromosome number, and in several cases can be transferred from one species to another ; many characters segregate in groups which are probably determined by groups of factors, since separation of these characters occasionally occurs ; types (combinations of characters) are associated with chromosome number ; new types arise, and generally variation exceeds the limits set by the two parents. He has attempted to explain these facts in accordance with mendelian principles and with cytological behaviour.

From his explanation of the inheritance of waxy it seems that the paired and unpaired chromosomes carry a similar series of factors. He therefore assumes that the tetraploid *turgidum* has 2 similar series of factors represented by $\mathbf{A}_1\mathbf{A}_2$, and the hexaploid *vulgare* has 3 similar series $\mathbf{A}_1$ $\mathbf{a}_2$ $\mathbf{A}_3$. This is in agreement with Winge's hypothesis that in these polyploids each of the sets of 7 chromosomes are more or less similar. $\mathbf{A}_3$ is supposed to be carried by an unpaired chromosome. Now, *e.g.*, in the cross $\mathbf{a}_1\mathbf{a}_2 \times \mathbf{a}_1\mathbf{a}_2\mathbf{A}_3$ the character would be associated completely with chromosome number unless the extra chromosome carrying $\mathbf{A}_3$ paired with one of the others. In the cross $\mathbf{a}_1\mathbf{A}_2 \times \mathbf{a}_1\mathbf{a}_2\mathbf{a}_3$ the character would be easily transferred. $\mathbf{a}_1\mathbf{A}_2 \times \mathbf{a}_1\mathbf{a}_2\mathbf{A}_3$ would give rise to $\mathbf{a}_1\mathbf{a}_2$ with a new character and to a form $\mathbf{a}_1\mathbf{A}_2\mathbf{A}_3$ where the character might be more highly developed than in either parent. Association between chromosome number and type he explains by assuming that the **A** symbols represent different groups of linked factors. As an example, he takes the case where the characters keeled and round glumes are not themselves associated with chromosome number but the combination of characters which goes along with them is associated with chromosome number. He shows diagrammatically how keeled and round can be transferred and how the round-glumed 28 and 42 chromosome segregates differ in type and also how the keeled-glumed 28 and 42 chromosome segregates differ in type (Fig. 53).

Nicotiana. Clausen (1928*a*) recognises twenty distinct species of *Nicotiana*, of which the somatic chromosome numbers are 18, 20, 24, 36 ?, 48, or 72 (the hybrid *digluta*). The majority of the species, however, have 24 or 48 chromosomes.

Hybrids between species within each of the three classes, $2n = 18$, 20 and 48 are fertile and their meiotic behaviour is normal. The following pairing behaviour is found at meiosis in hybrids between certain of these species (Clausen, 1928*a,b*).

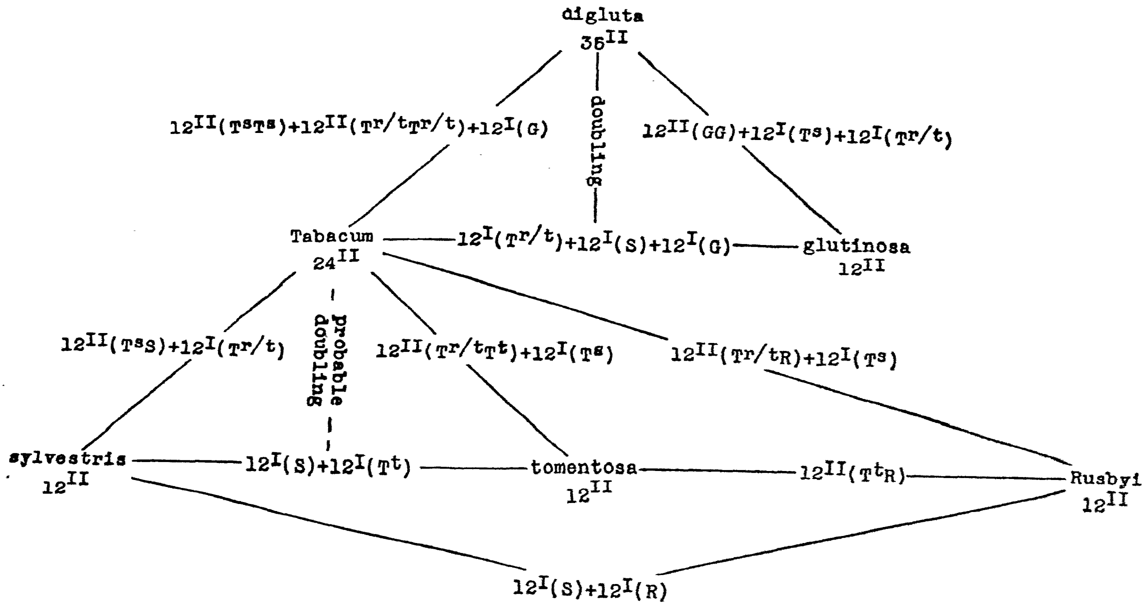


FIG. 54.

T^s = *Tabacum* homologues of *sylvestris* chromosomes S.
T^r = *Tabacum* homologues of *Rusbyi* chromosomes R, which are presumably homologous with the *tomentosa* chromosomes T^t, hence $T^{r/t}$.
G = *glutinosa* chromosomes.

The trispecific hybrid having the haploid complement of all three species (*N. Tabacum* × *N. Rusbyi*) × *N. sylvestris* gave 24^{II}, which may be interpreted as

Tabacum		*Rusbyi.*		*sylvestris.*	
$12\,T^r + 12\,T^s$	+	12R	+	12S	$= 12^{II}(T^r R) + 12^{II}(T^s S)$.

Close pairing	*paniculata-rustica*	($2n = 24 \times 2n = 48$)
	sylvestris-Tabacum	($2n = 24 \times 2n = 48$)
	tomentosa-Tabacum	($2n = 24 \times 2n = 48$)
	Rusbyi-Tabacum	($2n = 24 \times 2n = 48$)
	tomentosa-Rusbyi	($2n = 24 \times 2n = 24$)
Loose pairing	*glauca-Tabacum*	($2n = 24 \times 2n = 48$)
	glutinosa-Tabacum	($2n = 24 \times 2n = 48$)
No pairing	*sylvestris-tomentosa*	($2n = 24 \times 2n = 24$)
	glutinosa-Bigelovii	($2n = 24 \times 2n = 48$)
	sylvestris-Rusbyi	($2n = 24 \times 2n = 24$)

By intercrossing various species, Goodspeed and Clausen and their co-workers have come to some definite conclusions as to the relationships between the chromosome sets of several species. Fig. 54 shows the cytological behaviour of the F_1 hybrids between these species (Goodspeed and Clausen (1928), Clausen (1928*a,b*) and Brieger (1930)). It also shows the presumed relationships between the different chromosome sets, the manner in which the hybrid *digluta* arose and the probable origin of *N. Tabacum.* Below the diagram is the interpretation of the pairing behaviour of a trispecific hybrid having chromosomes contributed by all three species (*N. Tabacum* × *N. Rusbyi*) × *N. sylvestris* (Brieger, 1930).

No pairing takes place among the twenty-four chromosomes in the haploid *N. Tabacum.* This indicates that the two sets of twelve chromosomes are of different phylogeny (Chipman and Goodspeed (1927), Clausen and Mann (1924)). Further, this confirms the view that the haploid complement of *N. Tabacum* consists of one set *Tr* of twelve chromosomes corresponding to the haploid complement of *tomentosa* or *Rusbyi* and one set *Ts* corresponding to that of *sylvestris*. Goodspeed and Clausen (1928) point out that *N. sylvestris* and *N. tomentosa* are morphologically different, whereas *tomentosa* and *Rusbyi* are similar. They assume therefore that *Tabacum* arose by doubling of the chromosomes in a hybrid between *sylvestris* and *tomentosa* or close allies of these species. This was followed by genetic differentiation in both the hybrid and the ancestral stocks, but the differentiation was not sufficient to destroy the homology between the chromosomes.

Other cases of a similar type are *Galeopsis Tetrahit*, *G. bifida*, *Salix neocinerea*, *S. Laurina* (Heribert-Nilsson (1918) and Håkansson (1929*a*)), *Phleum pratense* (Gregor and Sansome (1930) and Gregor (1931)), *Spartina Townsendii* (Huskins, 1930), *Æsculus carnea* (*A. Hippocastaneum* × *A. pavia*) (Skovsted, 1929), *Rosa Wilsonii* (*R. pimpinellifolia* × *R. tomentosa*) (Blackburn and Harrison, 1924), *Dahlia variabilis* (Lawrence, 1929, 1931*a*) and polyploid wheat and oats (see pp. 298-305).

The hybrid polyploid forms which have arisen in experimental material, *Primula Kewensis*, *Digitalis mertonensis*, *Saxifraga potternensis*, *Rubus* RT$_4$, *Solanum nigrum* × *S. luteum*, *Euchlaena* × *Zea* (Emerson and Beadle, 1930), *Ægilops* × *Triticum* (Tschermak, 1926), *Brassica napocampestris* (Frandsen and Winge, 1932) and *Crepis artificialis* (Collins, Hollingshead and Avery, 1929), are also similar; cytological and genetical differentiation might possibly take place in the same way as presumed in the above natural hybrid polyploids.

When the chromosome constitutions of the parental species are known the meiotic behaviour of the chromosomes in the interspecific hybrids can be understood.

It will be noticed that the chromosome behaviour of the hybrids between *digluta* and *Tabacum* or *glutinosa* is similar to that of the hybrids between *Tabacum* and *sylvestris*, *tomentosa* or *Rusbyi* and between *N. paniculata* and *N. rustica* (Goodspeed, Clausen and Chipman, 1926) (*cf.* Fig. 54 and p. 312).

The homology of the chromosome sets in these species leads to characteristic phenomena in relation to fertility, breeding behaviour and survival of the allopolyploids.

For example, the hybrid from *digluta* × *Tabacum* (*digluta* will not hybridise with *Tabacum* or *glutinosa* when used as a male) is highly fertile, whereas the hybrid from *digluta* × *glutinosa* is sterile. The homology of the chromosomes in the first case is such that 24II and 12I are formed at meiosis, while in the second case 12II and 24I are formed (see Fig. 54). The behaviour of the univalents during meiosis (random assortment and occasional elimination—see p. 230) leads to a range in the chromosome numbers of the gametes of the F$_1$s. It is also found that the univalents which succeed in entering a gamete are further eliminated by inviability of the gametes.

Therefore either by selfing the F_1, *digluta* × *Tabacum*, or by crossing it to *Tabacum*, the *glutinosa* chromosomes are eliminated in a few generations (Clausen, 1928*b*). If *digluta* arose in nature it would remain constant until it hybridised with *Tabacum* when the hybrids would give rise to a preponderance of *Tabacum*-like forms.

Complete pollen sterility is characteristic of the *sylvestris-Tabacum* F_1 hybrid. Goodspeed and Clausen (1927*a*) found that most of the progeny of this cross had from 0—3 univalents in addition to the bivalents and only two plants had all twelve univalents. In the progeny of the *paniculata-rustica* hybrid twelve univalents were frequently found and the univalents were eliminated less frequently. In both cases the behaviour of the chromosomes at meiosis is similar, but the balance and viability of the gametes is different and gives differences in the genetic results.

There are many varieties of *N. Tabacum*, and Goodspeed and Clausen (1917) and Brieger (1928*b*) found that the morphology of the F_1 hybrid between *Tabacum* and *sylvestris* was affected by the particular variety of *Tabacum* used. The hybrids resemble an enlarged *Tabacum* variety with the addition of some *sylvestris* characteristics. A genetical study of the hybrids can only be made by back-crossing, since they are male sterile. When back-crossed with *sylvestris* two classes were found among the progeny :—

(1) A large group of highly variable aberrant forms which were almost sterile when selfed.

(2) A smaller group of forms more similar to *sylvestris* which were partially fertile. Later generations from these plants gave progeny which were completely fertile and identical with *sylvestris*.

In contrast to the original F_1 *Tabacum-sylvestris*, where the chromosomes formed 12 *Ts.S* bivalents and 12 *Tr.* univalents at first metaphase, the progeny of the back-cross to *sylvestris* would form 12 *SS* bivalents and a variable number of *Ts* and *Tr* univalents.

When the F_1 *sylvestris-Tabacum* was back-crossed with *Tabacum* the progeny could be grouped into three classes.

(1) A large group of aberrant forms which were sterile when selfed ;

(2) A few forms like *Tabacum*, which were almost sterile ;

(3) A few forms like *Tabacum*, which were partially fertile, and

among whose progeny were fertile lines identical with the original *Tabacum*.

Any products of recombination formed in the F_1 hybrid are apparently soon eliminated in the succeeding generations.

If p = number of *Tr* univalents eliminated in the gametes of the F_1.
q = ,, *Ts* ,, in the F_1 gamete.
and $12\text{-}q$ = ,, *S* ,, ,, ,,
where p and $q = 12 - 0$, the chromosomal constitution of the progeny of the back-cross F_1 *Tabacum-sylvestris* × *Tabacum* may be represented thus—$qTsTs$ bivalents + $(12\text{-}q)TsS$ bivalents + $(12\text{-}p)TrTr$ bivalents + pTr univalents.

We suggest, therefore, that the first class above corresponds to those forms which arise from F_1 gametes containing less than 12 *Tr* univalents and a variable number of *Ts* chromosomes. Class (2) contains those with the majority of *Tr* and *S* chromosomes, while class (3) contains the majority of *Tr* and *Ts* chromosomes.

Goodspeed and Clausen found that *sylvestris*-like derivatives of the *Tabacum-sylvestris* hybrid behaved in a similar manner to that of pure *sylvestris* when further crossed with *Tabacum*. One exception, however, was found. When one *sylvestris* derivative was crossed to the *Tabacum* var. *purpurea* parent which was used in the original cross, half the progeny had the characteristic *purpurea* type of leaf base. They supposed that the *sylvestris*-like derivative from the cross *Tabacum* var. *purpurea* × *sylvestris* contained a chromosome, or part of a chromosome, derived from the *Tabacum* var. *purpurea* parent.

Watkins (1925) considers that the *Ts* and *sylvestris* chromosomes which pair in the F_1 hybrid are genetically similar, and that the 12 *Tr* chromosomes contain the differential factors for the *Tabacum* species. Replacement of the *Ts* chromosomes by *sylvestris* chromosomes therefore will not have a great effect on the phenotype of *sylvestris*-like derivatives. Naturally, where *Ts* and *S* contain allelomorphic factors, replacement will demonstrate this difference, *e.g.*, *purpurea* type of leaf base. In the progeny of the F_1 back-crossed to *Tabacum*, the *Tabacum*-like plants will have received (from the F_1 parent) most of the 12 *Tr* chromosomes which carry the special *Tabacum* factors ; the aberrant forms will have obtained

Ts and *S* chromosomes along with one or more of the 12 *Tr* chromosomes from the F_1 parent. The differences in morphological characters are mainly due to the difference in the number of *Tr* chromosomes present.

Webber (1930*b*) made a cytogenetic study of a hybrid between *Tabacum* and *sylvestris* which had 60 chromosomes, *i.e.*, the somatic complement of *Tabacum*, $2Ts + 2Tr$ and the haploid complement of *sylvestris*, *S*.

This form was chromosomally unbalanced and gave rise to many new chromosome combinations in the progeny. In appearance it did not differ greatly from its sister triploid F_1s, but was much more fertile. The increase in the proportion of *Ts* and *S* chromosomes in comparison with *Tr* was not, therefore, reflected in the external morphology ; the effect of the *Tr* chromosomes gives apparent support to Watkins' view. Evidence, however, has been furnished by Webber that a few of the *Ts* chromosomes contain factors controlling *Tabacum* characteristics.

Later generations from the 60 chromosome hybrid show that elimination of the *sylvestris* chromosomes may or may not be accompanied by phenotypical change. This indicates that the *Ts* and *S* chromosomes may be similar, but not identical, in genetic content.

The production of pink flowers, presumably by exchange of homologous chromosomes between the two species, has been observed in the back-cross (*sylvestris* × *Tabacum*) × *sylvestris*, by Goodspeed and Clausen, and in derivatives of the polyploid F_1 *sylvestris* × *Tabacum*, by Webber.

Later generations of the 60 chromosome hybrid between *sylvestris* and *Tabacum* showed considerable variation in morphology. These plants had generally 24 or 25 bivalents. These differences follow from multivalent association between the *Ts* and *S* chromosomes and replacement of *Ts* by *S* homologues. The former type of plant might be considered to be a variety of *Tabacum*, but the latter had distinct *sylvestris* characteristics. Hence, as the result of forming a complex polyploid which would not survive in nature, forms can be created, distinct in type, which have a new basic number of chromosomes, and are fertile. In this particular case, the twenty-five bivalent forms would not long remain distinct if in contact with *Tabacum*, since hybridisation would reduce them to *Tabacum*. In isolation, however, such a form might easily become differentiated sufficiently to ensure that when it again came into contact with *N. Tabacum* it would not hybridise.

The hybrids between *N. rustica* and *N. paniculata* show a general similarity in behaviour to the hybrids between *Tabacum* and *sylvestris* and between *digluta* and *Tabacum*, but the particular differences between the first two and the second two examples are of interest.

As a result of the cytogenetic studies of Goodspeed, Clausen and Chipman (1926), Lammerts (1929, 1931) and East (1921) the constitution of *N. paniculata* ($2n = 24$) may be represented as 12 *PP* bivalents and that of *N. rustica* ($2n = 48$) as 12 *RpRp* and 12 *RR* bivalents.

The hybrid forms 12 *PRp* bivalents and 12 *R* univalents at first metaphase and produces gametes containing 12–24 and sometimes 36 chromosomes in frequencies expected on random assortment of the chromosomes. Lammerts and East back-crossed the F_1 with *rustica* reciprocally and found that 32% of the viable egg cells contained the somatic number of chromosomes. On the male side the functional gametes of the F_1 contained 18–24 chromosomes, but gametes with 23 and 24 chromosomes were most frequent. All the plants with 24 bivalents were fertile but were variable in appearance —some resembled the *rustica* parent while others indicated that some *paniculata* homologues had been transmitted from the F_1 hybrid. In addition a range of plants was found with 18 bivalents and 6 univalents to 23 bivalents and one univalent. These plants (246 in number) fell into two groups: (1) a very large group which resembled *rustica* in general characteristics and was equal to or greater than the F_1 in fertility. (2) four plants which were almost identical with *paniculata*. Two were sterile and two were fertile.

The third intermediate group corresponding to the intermediate group in the progeny of the back-cross (*sylvestris-Tabacum*) × *Tabacum* was absent. Later generations from plants in both groups were more fertile and more similar to *rustica* and *paniculata* respectively. It was found that the *rustica*-like group varied in a manner similar to *rustica* itself, which is known to exist in a number of distinct varieties. Indeed, some of these plants resembled particular varieties of *rustica* which had not been used in the cross. Lammerts (1931) has made an extensive cytological examination of these progenies. He found that in viable zygotes the sum of the number of bivalents and univalents formed was equal to the haploid number of the tetraploid parent *rustica*—24. This is similar to Kihara's explanation of the behaviour of hybrid pentaploid wheat derivatives. The F_1 hybrid is of the constitution *RpPR* and when crossed with *rustica*, which produces gametes containing *RP*, we expect in the progeny 12 *PP* bivalents, together with *RR* and *RRp* bivalents and *R* and *Rp* univalents. As in the *sylvestris-Tabacum* hybrid the relative number of bivalents and univalents depends on the number of *R*, *Rp* and *P* chromosomes transmitted from the hybrid.

The *Tabacum-sylvestris* F_1 is less variable than *N. rustica* and it is probable that the hybrid *rustica-paniculata* will produce more viable and variable progeny than the *Tabacum-sylvestris* F_1.

The experiments in *Nicotiana*, *Galeopsis*, wheat, oats, *Phleum*, *Primula Kewensis*, *Rubus* and others are informative on several points of biological importance.

The wild species, *Galeopsis Tetrahit*, *Nicotiana Tabacum*, *Nicotiana rustica*, *Phleum pratense* (6*x*), *Salix cinerea*, *Rosa Wilsonii*, *Spartina Townsendii*, *Dahlia variabilis* and other species, are shown to have been evolved by hybridisation and polyploidy.

Most of these forms have chromosomes which are not greatly differentiated from those of the original parents. Where the two original parental species of a polyploid hybrid have no homologous parts of chromosomes the polyploid hybrid will have total autosyndesis and full fertility. Such forms are *Raphanus-Brassica*, *Nicotiana Tabacum* and *N. digluta*. If a hybrid can be obtained between two species it is probable that these species are related to some extent and have had common ancestors. It is therefore expected that parts of the respective chromosome complements will be homologous since the chromosomes will be of the same origin. Allosyndetic pairing will occur with respect to these parts. Any differentiation of the chromosomes of the parental species which has taken place since the two species originated, may therefore be measured by the amount of allosyndesis occurring in the immediate polyploid hybrid between them. *The amount of differentiation will* *be inversely proportional to the amount of allosyndesis.* Thus in *P. Kewensis* one and at most three quadrivalents are formed while in *Galeopsis* artificial *Tetrahit* and pseudo-*Tetrahit* (3*x*) trivalents are formed occasionally, and in the artificial hexaploid of *Phleum pratense* × *P. alpinum* multiple associations of chromosomes are found.

As already pointed out, allosyndesis in such a hybrid leads to reduction in fertility. Further, crossing-over between homologous parts of otherwise non-homologous chromosomes will lead to the recombination of factors and to interchange, translocation and hence to reduplication and deficiency. Sterility is associated with these chromosomal abnormalities and natural selection will probably eliminate such forms. On the other hand, recombination will enable new balances to be set up which may be favoured by selection on the ground that they are accompanied by the appearance of a character valuable to the plant. Such may be the cause of the appearance of small flowers in the tetraploid *Galeopsis* when the two diploid and related species have large flowers. Müntzing found that the triploid and tetraploid forms of *Tetrahit* had greater variability in flower size than the parents, but that the natural species had less variation.

The fact that newly-formed polyploids often show greater variability in zygotic and gametic sterility than their succeeding generations may be explained therefore on the above basis. Obviously the degree of homology between the chromosome sets derived from each parent is of great importance in determining the genetic behaviour of a new polyploid. There may be some polyploid species hybrids which exhibit the phenomena of structural hybridity. The differentiation of the chromosomes of the two parental species may be both genetical and structural. In a polyploid hybrid, the presence of a previous segmental interchange may therefore be brought to light.

Back-crossing a polyploid hybrid with the parental species usually produces a plant with an uneven number of chromosomes. Consequently this hybrid is comparatively sterile and gives rise to progeny ranging in type and chromosome number. Some of these derivatives, however, may have a relatively high survival value. For example, the plants with 25 bivalents which result from the polyploid hybrid between *Tabacum* and *sylvestris* might be the progenitors of several species of *Nicotiana* with a new basis chromosome number. Naturally, of course, the origin and survival value of these forms are dependent on the genetic balance. The difference in behaviour of the hybrids between *N. Tabacum* and *sylvestris* as compared with that of the hybrids between *N. rustica* and *paniculata* is probably due to their different balance.

The gain or loss of a chromosome in polyploids has much less effect on the balance than in diploids. Thus in a polyploid such as *N. Tabacum* aneuploidy might be expected more frequently than in the supposed diploid parental species. Plants with a chromosome deficiency are extremely rare in diploids. $6x - 1$ or $6x - 2$ forms of wheat and oats are known, and Goodspeed and Clausen (1926*a*,*b*), Goodspeed and Avery (1933), Lammerts (1932), Olmo (1935), have described $4x - 1$ forms of *N. Tabacum*. The monosomic forms, "corrugated" and "fluted," were found in a *Tabacum*-*sylvestris* hybrid and in *Tabacum* respectively. About 60% of the eggs and 3% of the pollen containing the chromosome deficiency are functional. The particular chromosome homologous to that which is deficient in "corrugated" must bear a dominant factor for red flower, since 31% of coloured plants were obtained on crossing "corrugated" with white *N. Tabacum* and 98–100% of coloured forms on crossing normal sister plants with white *Tabacum*. Forms are even known which have no "fluted" chromosome (nullo-*F*) or no "corrugated" chromosome (nullo-*C*).

In a progeny of a selfed haplo-fluted plant which had carmine flowers (Co) a coral-flowered (co) plant was found (Clausen, 1930). This plant bred true for coral flowers. By crossing normal coral plants with fluted carmine plants the combination fluted and coral was obtained. It will be remembered that "fluted" has the chromosome constitution of 23 bivalents and one univalent. It was found that the univalent contained the alternative factors or factor complexes for carmine and coral. Sometimes in the hybrid between fluted carmine and normal coral a plant was obtained which was variegated for the coral and carmine flower colours. Cytological examination showed that the normal plants had 24 bivalents, the fluted plants 23 bivalents and one univalent, while the variegated plants had a fragment in addition to the complements of normal or fluted plants. This fragment appears to be about one fifth of the size of the fluted univalent and has been seen to behave irregularly at division of the nucleus. This evidence shows that the fragment is a part of the fluted univalent and contains the factor or factor complex for coral and carmine flower colour. When the fragment is present carmine flower colour will be produced but in its absence the coral flower colour will be found in plants with the coral complex on the fluted chromosome. The variegated condition arises through the irregularity of the behaviour of the fragment during mitosis.

If we designate the chromosome which is deficient in "fluted" plants as *F* and the fragment of *F* which bears **Co** as *f*, the constitution in respect of the *F* chromosome of the plants can be written:

normal coral (24II) *F*-**co** *F*-**co**,
"fluted" coral (23II + 1I) *F*-**co**,
normal, heterozygous carmine, coral variegated plant
(24II + 1*f*) *F*-**co** *F*-**co** *f*-**Co**,
"fluted" heterozygous carmine, coral variegated plant
(23II + 1I + 1*f*) *F*-**co** *f*-**Co**.

This example is of great interest since it illustrates the effect of chromosome fragmentation upon factor inheritance and upon variegation in the somatic tissue.

Indeed Clausen (1932) found five wholly carmine plants in the progeny of carmine coral plants. These reversions from a variegated form, of the constitution *F*-**co** *F*-**co** *f*-**Co**, indicate that in some way **Co** (carmine) has become stabilised. The reversion of mutated endosperm characters in maize investigated by Stadler (see p. 125), and the behaviour of genes in maize (see p. 116), may be considered along with this case.

Crepis. Genera such as *Crepis*, *Carex*, *Viola*, *Salix*, and *Rosa* have been extensively studied from the point of view of species differentiation. In these investigations the genetics, cytology and taxonomy of the species have been taken into consideration. These genera exhibit some of the phenomena already seen in *Nicotiana* as well as characteristics peculiar to each of them.

In *Crepis* and *Carex* changes in chromosome number and morphology are frequent. Chromosome numbers in *Crepis* species include $2n = 6$, 8, 10, 12, 14, 15, 16, 22, 33, 40, 44, 55 and 88, but about three-fifths of all the species have the somatic number of 8, and about one-fifth of the species have the chromosome number 10. *Crepis capillaris* and *fuliginosa* are distinct among the higher plant organisms in having the low chromosome number $2n = 6$ (Babcock and Cameron, 1934).

At least six interspecific hybrids of *Crepis* have been observed to occur in nature. Certain of these occur not infrequently, and the fact that interspecific hybrids may be obtained artificially with comparative ease indicates that in nature, where different species occur together, hybridisation may not be uncommon. Artificial hybrids in about 100 different combinations involving 36 species have been obtained by various workers. Only about one-fifth of these hybrids are fertile to any extent under natural conditions, and these are mostly hybrids between closely related species. A table compiling results obtained by the various workers is given by Babcock and Navashin (1930). The study of this group of partially fertile hybrids substantiates the close morphological relationships observed between the parental species. Many hybrids which are almost sterile can be back-crossed successfully. In this way it has been possible to study them and their derivatives both genetically and cytologically. In general where one parent has more chromosomes than the other, the characters of the parent with the higher chromosome number predominate in the F_1.

Collins and Mann (1923) obtained vigorous hybrids between the species *C. biennis* ($2n = 40$) × *C. setosa* ($2n = 8$). The F_1 possessed characters mostly resembling *C. biennis* and contained 20 *biennis* chromosomes and 4 *setosa* chromosomes. In meiosis 10 bivalents and 4 univalents were formed regularly, indicating that the chromosomes of the *biennis* haploid complement paired among themselves, *i.e.*, autosyndesis. In view of this they predicted the possibility of obtaining constant fertile forms containing chromosomes derived from both species. This prediction was fulfilled (Collins, Hollingshead and Avery, 1929). The F_2 plants were very heterogeneous—those most like *biennis* being most fertile. One F_4 plant was found to breed true, and since it possessed characters distinct from other species it was given specific rank and termed *C. artificialis.*

It formed a link between two subgenera *Eucrepis* and *Barkhausia.* The chromosome complement of *C. artificialis* was found to consist of 10 pairs of *biennis* chromosomes plus two pairs of *setosa* chromosomes. The two pairs of *setosa* chromosomes could be recognised from their morphology (Fig. 55). At first metaphase 12 bivalents were observed—autosyndesis accounting for its breeding true. On back-crossing *artificialis* with *setosa*, it was found that 7 bivalents

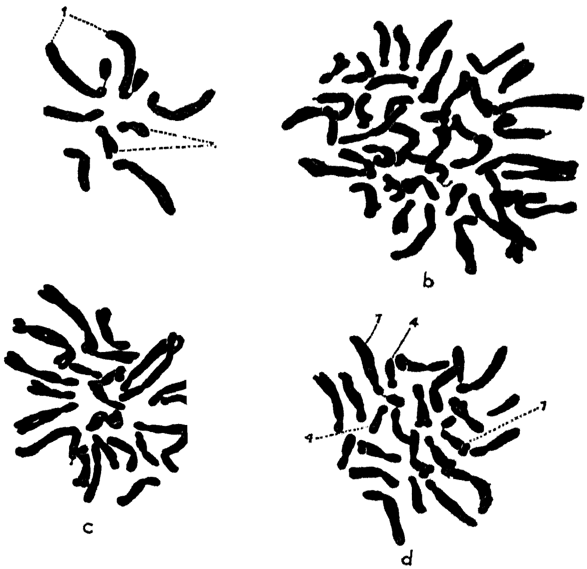


Fig. 55. Somatic chromosomes of *a*, *Crepis setosa* ($2n = 8$); *b*, *C. biennis* ($2n = 40$); *c*, F_1 hybrid *C. setosa* × *C. biennis* ($2n = 24$); *d*, *C. artificialis* ($2n = 24$); the 2 pairs from *setosa* are numbered as in *a*. (Collins, Hollingshead and Avery, 1929.)

and 2 univalents were formed in the derivatives, and therefore autosyndesis must have taken place in the case of the 10 *biennis* chromosomes. Further evidence of this form of internal pairing among the 10 *biennis* chromosomes was obtained from the progeny of an F_1 back-crossed with *biennis.* In this case some plants received no *setosa* chromosomes from the hybrid parent, and since 15 bivalents were formed, the 10 *biennis* chromosomes from the hybrid parent must have formed five pairs. From this evidence it is concluded that *C. biennis* is an octoploid species containing eight sets of five chromosomes, although each kind of chromosome is probably not present eight times. The distinctive size and vigour of this species as compared with other species also substantiates the view that it is polyploid. Up to the present no species of *Crepis* have been recognised as the forms from which the polyploid *biennis* may have originated.

In *C. artificialis* we have an example of a new species which has appeared suddenly by hybridisation and not through gradual changes. An essential feature in the meiosis of *C. artificialis* is the autosyndetic chromosome pairing, which results from the polyploid nature of one of the parent species.

Triploids have been observed by Navashin (1925*b*, 1926, 1929*a,b*) in the following species, *C. capillaris*, *C. tectorum*, *C. dioscoridis* and *C. parviflora*. He believes that they arose by fusion of an egg containing the diploid number of chromosomes, with a normal male gamete. Tetraploids were found in *C. tectorum* and a pentaploid in *C. capillaris*.

On selfing triploids the progeny consisted mainly of diploids and triploids and a few single and double trisomics and higher grades of polyploids. Using these triploid forms as females in crosses with other diploid species, Navashin (1927*b*, 1929*a*) obtained hybrids containing two, three and four maternal haploid groups along with the haploid paternal group. F_1 interspecific hybrids, when allowed to hybridise with the parental species and when sufficiently fertile, were found by Navashin (1927*b*, 1928, 1929*b*) to give mainly triploids and diploid hybrids in the progeny (when a third species is present trispecific hybrids are sometimes produced). A few recombination products and higher polyploids occur. The triploids contain two haploid groups of one parent and one haploid group of the other parent; the diploids are either like the pure parental species or identical with the F_1 hybrid. The higher polyploids may have, for example, three haploid sets from one species with either one or two haploid sets of the other species. In three cases interspecific hybrids containing the diploid complement of each parent have been obtained, viz.,

2 *capillaris* + 2 *dioscoridis* (Navashin, 1929*b*)
2 *capillaris* + 2 *tectorum* (Hollingshead, 1930*b*).
2 *rubra* + 2 *fœtida* (Poole, 1931).

The latter tetraploid hybrid was the only one which was somewhat fertile—an unusual result, since most polyploid hybrids in *Crepis* and similar tetraploids in other genera are partially fertile.

Trispecific hybrids usually (i.) are gigantic, especially so if they contain two or more haploid sets of one parent, (ii.) show characters of all three species, and (iii.) are sterile.

There is, therefore, no lack of evidence of chromosome doubling, either in the species itself or through hybridisation, and the fact that a tetraploid interspecific hybrid which is somewhat fertile has been produced tends to support the possibility of chromosome doubling having given rise to the higher numbers in the series. On the other hand, when an attempt is made to utilise this evidence in the theoretical reconstruction of the species, it meets with little success.

Among the progeny of a triploid hybrid of *C. capillaris* × *C. tectorum* Hollingshead (1930*b*) found a class containing the diploid *capillaris* chromosome complement together with various combinations of *tectorum* chromosomes. Like trisomics, these were of low viability and tetrasomics did not occur. This evidence is against the idea that species with the addition of chromosomes may arise in this way, but is not conclusive since all species may not behave in this manner.

The genetics of several diploid species has been studied, *C. capillaris* ($2n = 6$), Babcock and Collins (1922*a*,*b*), Rau (1923), Collins (1924), *C. dioscoridis* ($2n=8$), Collins (1926), Haney (unpub.), *C. fœtida* ($2n = 10$), Haney (unpub.), *C. neglecta* ($2n = 8$), Avery (unpub.), *C. rubra* ($2n = 10$), Haney (unpub.) *vide* Babcock and Navashin (1930), *C. tectorum* ($2n = 8$), Collins, *vide* Babcock (1922), and in each case the pairs of characters were found to segregate in a mendelian manner. Factor mutation has probably played a part in the formation of the numerous polymorphic species in the genus.

The view that factor mutation only produces pathological effects and cannot therefore play a part in evolution is quite untenable, for besides other examples given throughout this book many of the allelomorphic characters studied in *Crepis* have no effect whatsoever on the viability and fertility of the plant.

An interesting contrast is shown by *C. capillaris* where hairy involucre is dominant to hairless involucre, while in *C. neglecta* and *C. bursifolia* for the same characters the dominance is reversed.

On crossing two distinctly different forms of *C. capillaris*, *C. tectorum* or *C. rubra* (Haney, unpub.), respectively, it was found that the F_1s were only about 50% fertile and the F_2s were highly variable. This evidence indicates that in species of wide geographic distribution, factor mutation and structural rearrangement may have produced extreme types and this process together with the aid of isolation may eventually produce forms of specific rank. Further evidence that factor mutation has played a part in the evolution of *Crepis* was obtained by Collins (1921). On crossing two different races of *C. capillaris* both races having no paleæ on the receptacle (a character which is almost universal in *Crepis*), he found types among the hybrids having paleæ on the receptacle. Moreover, this recessive reversionary character was inherited in a simple mendelian manner. Presence of paleæ is phylogenetically older than its allelomorph, absence of paleæ. It is therefore probable that a step in the evolution of *Crepis* has been made through the dominant factor mutation for absence of paleæ.

An interesting interspecific lethal factor has also been discovered in *Crepis*. Babcock and Collins (1920*a*) and Navashin (1926) crossed *C. capillaris* with *C. tectorum* and obtained hybrids which died in the cotyledon stage. Later Navashin (1927*b*) succeeded in obtaining viable hybrids, whilst Haney (unpub.), using different plants of each species, obtained five families, one of which produced twenty mature plants, the other four families dying at the cotyledon stage. Hollingshead (1930*a*) investigated this behaviour and found that some plants of *C. tectorum* contained a factor, either in the homozygous or heterozygous condition, which did not affect the germination, but was lethal to the development of hybrids between *C. tectorum* and *C. capillaris*. This lethal was also effective in hybrids of *C. tectorum* with *C. bursifolia* and *C. leontodontoides*, but probably ineffective in hybrids between *C. tectorum* and *C. setosa* or *C. taraxacifolia*. The races of *C. tectorum* used in this experiment were of wild origin and from regions widely separated so that this factor mutation took place either early or frequently in the evolution of this species.

The cytological study of *Crepis* species, Babcock and Collins (1920), Collins and Mann (1923), Mann (1925), Taylor (1925), Navashin (1925*a*,*b*, 1926, 1927*a*,*b*, 1928, 1929*a*,*b*, 1931*a*,*b*,*c*), Babcock and Mann Lesley (1926), Hollingshead (1930*b*), Hollingshead and Babcock (1930), Collins, Hollingshead and Avery (1920), Babcock and Clausen (1929), Avery (1930) and Rosenberg (1928), Richardson (1935), Babcock and Cameron (1934), Babcock and Emsweller (1936), indicates a further method of species evolution —namely, structural change of the chromosomes.

By comparing the somatic chromosome complements of different species with regard to their number, morphology and size, some insight is obtained regarding the relationships between the species and the processes which have given rise to the differentiation.

Particular attention has been paid to morphological characteristics of the somatic chromosomes such as the position of the attachment constriction, the presence and absence of satellites and also differences in size. In this way it has been possible to recognise each of the pairs of homologous chromosomes in most of the species.

The majority of *Crepis* species differ from their closer relatives in the morphology of the chromosomes and not in the number of chromosomes. That these morphological characteristics of the chromosomes are constant has been amply proved. Thus in interspecific *Crepis* hybrids it has been shown that the parental chromosomes appear unaltered in the hybrid. Incidentally, this affords further proof that the chromosomes retain their individuality. A few exceptions to this rule have been discovered which usually consist of the loss of a satellite from a particular chromosome. This phenomenon is termed amphiplasty. An example of this is to be found in the F_1 hybrid between *C. capillaris* and *C. tectorum* where the satellite on the *tectorum D* chromosome is always lost, while the satellite on the *capillaris* chromosome is unaffected. This behaviour occurs whichever way the cross is made. On the other hand, in the F_1 hybrid between *C. capillaris* and *C. parviflora* the satellite is always lost from the *capillaris* chromosome. This behaviour is regarded as the result of the particular physico-chemical condition set up in the hybrid cell. Müntzing shows that the hybrid of *Crepis divaricata* and *dioscoridis* ($n = 4$) contains evidence of structural differences between the chromosomes of the two species, while Richardson (1935) finds structural difference in a race of *C. capillaris.*

It has been found that morphologically similar species of *Crepis* have similar chromosomes, a condition which is associated with a common phylogenetic origin. There is one exception where a group of species far removed phylogenetically have similar chromosomes.

Changes have taken place during the process of evolution with regard to chromosome shape. Races occur within species which differ from the type in the shape of one pair of chromosomes (position of attachment constriction) and others occur which possess a heteromorphic pair of chromosomes. Another species may be divided into three races in respect of their chromosomes bearing satellites. One race has two large satellites, one has two small satellites and one has unequal satellites on the pair of homologous chromosomes. These satellites remain unchanged in later generations. This evidence indicates that changes in shape are not uncommon.

Differences in size and number of the chromosomes must also have occurred. Generally increase in number is associated with increase in length. Differences in length may occur with regard to the total length of all the chromosomes (*i.e.*, chromatin mass, for all *Crepis* chromosomes are of about the same thickness) but may only affect individual chromosomes.

Navashin (1931*b*) has examined thirteen species and found that the cell volume is proportional to the amount of chromatin, *i.e.*, the size of the chromosomes. Thus it was proved that interspecific differences in the amount of chromatin have the same consequences as intraspecific differences where the diploid complement is increased by one or more haploid complements, *i.e.*, polyploidy.

Alteration in the chromosome number, *e.g.*, the addition of a pair of extra chromosomes does not appear to have taken place following previous non-disjunction since no diploid species of *Crepis* is known to have more than two homologous chromosomes associated. Further, the genetical evidence shows that trisomics are of low viability, and that tetrasomics do not occur. As already seen, however, increase in chromosome number through doubling of the chromosomes is a possibility.

Decrease in chromosome number, *e.g.*, elimination of a pair of chromosomes may result from irregularities at meiosis or from fusion of non-homologous chromosomes. No evidence of the former type is available in *Crepis*, and known cases of this type only occur in polyploids, *Triticum* (Kihara (1924, 1925), Huskins (1928*a*)), *Avena* (Huskins, 1927) and *Primula Kewensis* (Newton and Pellew, 1929). The plants moreover were partially or wholly sterile. $2n-1$ plants have never been discovered in *Crepis* and such types in *Datura* never gave rise to plants lacking a pair of homologous chromosomes. Possible evidence of fusion has been obtained in the discovery of a large V-shaped chromosome (Navashin, 1931*a*).

As has been already pointed out, most of the closely related species differ in morphological details of the chromosomes and not in chromosome number. These morphological differences are therefore regarded as being the most important factor in the differentiation of the species. As to how these differences take place the evidence is very meagre but suggestive of structural changes. There is no definite evidence for fusion but fragmentation of the chromosomes has been observed in three species of *Crepis*. In certain cases the fragmented chromosome has given rise to two functional chromosomes, and in one species plants containing fragmented chromosomes were partially fertile. In this way new specific chromosome sets may have originated. Large V-shaped chromosomes, which have been observed, have probably resulted through fragmentation and fusion.

Recent cytological investigations in other genera have shown that changes involving fragmentation, translocation, reduplication, inversion and deletion of parts of the chromosomes have taken place in the processes of evolution. These changes have also been artificially induced in *Crepis* (Navashin, 1931*c*) and in other plants by irradiation with X-rays. It would appear that in the evolution of *Crepis*, changes such as these, termed " transformations," have played an important part, resulting in differences in size and shape and to some extent in the number of chromosomes. Associated with these differences there would naturally be differences in external morphology through loss or gain of factors giving rise to a new factorial balance. In addition, factor mutation would play a part in the differentiation of the species without causing alteration of the chromosome complement. Polyploidy and interspecific hybridisation are also apparently involved in the creation of new species.

Transformation, however, is regarded by the *Crepis* workers as being the most frequent cause for the origin of new species of *Crepis*.

Viola (*vide* Clausen, 1931*a*). In the *Melanium* section of *Viola* are species with chromosome numbers ranging from $2n = 14$ to $2n = 60$, with intermediate numbers such as 20, 22, 26, 34, 36, 40 and 48.

Some relatively fertile interspecific hybrids have been obtained and by a genetic and cytological study of the group it has been possible to indicate in some measure the mode of evolution of the sub-genus.

Table 49 gives the cytological behaviour together with the fertility of some of the species hybrids. It can be seen that hybrids between species with different chromosome numbers were quite frequently obtained and that the F_1s were sometimes fertile (*e.g.*, the F_1 of *V. tricolor* × *V. arvensis*) and that succeeding generations were obtained. The chromosome behaviour in meiosis in the species hybrids is of particular interest. In crosses 1, 2, 3, 5, 6, 7, 10, 12, 13, 15, 16, 18 and 20, associations of more than two chromosomes were observed. In addition, several cases were noted where the chromosomes might be considered to be secondarily associated (see p. 324) although Clausen is unwilling to be definite on the matter.

It is of importance to note that multiple association of chromosomes occurred in the F_1s when only bivalents were formed in the parent species. An example of such a case is the F_1 of *V. cornuta* ($2n = 22$) × *V. elegantula* ($2n = 20$), in which trivalents and quadrivalents were formed. Probably this results from differences in the arrangements of the segments of the chromosomes, *i.e.*, the species hybrid is also a structural hybrid.

In other cases where the chromosome number of the hybrid is higher it is probable that both interchange and reduplication of chromosome parts are the causes of multiple association. The presence of univalents may arise either from too little or too much homology among the chromosomes. Trivalent formation or, when the frequency of chiasmata is low, failure to form trivalents or quadrivalents will lead to the appearance of univalents at metaphase.

Autosyndesis sometimes occurs in hybrids between species with

TABLE 49

List of successful Hybridisations in Viola. (*I, II, III denote univalents, bivalents, etc.*) (Clausen, 1931*a*).

Cross No.	Maternal Species	Paternal Species	Conjugation of Chromosomes in F_1	Fertility, Seeds per Plant, F_1	Germination	Carried to	Including Backcrosses to	F_1 cultivated Year	Remarks
1	*cornuta* n = 11	*elegantula* n = 10	ca. $10_{II} + 1_{I}$ $(1–6_{I})$, III + IV occur	300–500 not poor	poor, 9%	F_2	*elegantula*	1925	F_3 did not germinate
2	*elegantula* n = 10	*Orphanidis* n = 10, 11	multivalent association (III, IV, V, VI; I rare)	250–300, rather good	—	F_1	—	1930	spontaneous hybrid
3	*lutea* n = 24	*elegantula* n = 10	$14–15_{II}$, $6–4_{I}$ autosyndesis, polysomic chains formed	50–100, poor	poor	F_2	—	1928	poor flowering of F_1
4	*cornuta* n = 11	*orthoceras* n = 11	11_{II}, no elimination	rather good	poor	F_2	—	1927	—
5	*Orphanidis* n = 10, 11	*cornuta alba* n = 11	$8–11_{II}$, $8–0_{I}$, III and IV occur	200–400, rather good	poor, 10–20%	F_2	—	1927	F_3 weak
6	*tricolor alba*-yellow n = 13	*elegantula* n = 10	$8–10_{II}$, $7–3_{I}$, polysomes (III–VI) rather common	abt. 30, very poor	—	F_4	*elegantula* *tricolor*	1927	segregated cespitose sterile dwarfs
7	*tricolor alba*-yellow n = 13	*Orphanidis* n = 11, 10	$0–11_{II}$, $24–2_{I}$, some III and IV; I split often	30–130, poor	poor, 24%	F_4	*tricolor*	1927	—
8	*tricolor* n = 13 *alpestris*	*alpestris* n = 13 *tricolor*	13_{II}, rarely $2–4_{I}$; extranuclear nucleoli very common	1500–2000, very good	abt. 60%	F_2	—	1926, 1928	3 different reciprocal crosses

9	*tricolor* n = 13 *arvensis*	*arvensis* n = 17 *tricolor*	11–13$_{\text{II}}$, 8–4,	500–2000, very good	good	F_9	*tricolor, arvensis*	1921 and later	11 different reciprocal crosses
10	*tricolor alba* n = 13 *Kitaibeliana* n = 7	*Kitaibeliana* n = 7 *tricolor alba* n = 13	4–6$_{\text{II}}$, 12–8$_{\text{I}}$, occasional III	0–30, very poor	—	F_1	*tricolor*, 10–30 seeds per plant	1930	—
11	*tricolor alba* n = 13	*Kitaibeliana* n = 18	7–12$_{\text{II}}$, 17–7$_{\text{I}}$, non-reduction observed, I split often	20–50, very poor	not good, 23%	F_2	*tricolor*	1927	—
12	*tricolor alba* n = 13	*nana* n = 24	5–1$_{\text{I}}$, (= 16–18$_{\text{II}}$), III and IV occur; autosyndesis	1000–2000, very fertile	—	F_1	*tricolor*	1930	—
13	*tricolor alba*-yellow n = 13	*rothomagensis* n = 17	ca. 1$_{\text{IV}}$, 2–3$_{\text{III}}$, 3–6$_{\text{I}}$ (+bivalents), splitting elimination	12–37, very poor	poor 15%	F_4	*tricolor*	1927	—
14	*tricolor hortensis* n = 13 *lutea*	*lutea* n = 24 *tricolor*	8–11$_{\text{I}}$, mostly splitting conjugation often in irregular chains	50–300, rather poor	poor 10%	F_4	—	1925	*tricolor alba* × *lutea* less viable
15	*tricolor hortensis* n = 13 *Battandierii*	*Battandierii* n = 26–30 *tricolor*	few I; autosyndesis; III + IV	ca. 100, rather good	not good, 25%	F_2	—	1927	*tricolor alba*-yellow × *lutea* less viable
16	*arvensis* n = 17	*rothomagensis* n = 17	4–6$_{\text{I}}$, often splitting; 1–2$_{\text{III}}$, occasional IV; (+ II)	250–450, rather good	30%	F_2	—	1926–1928	reciprocal unsuccessful
17	*Kitaibeliana* n = 7	*arvensis* n = 17	most common: 6$_{\text{II}}$ + 12$_{\text{I}}$; up to 2$_{\text{II}}$ + 20$_{\text{I}}$; many I split	500–600, rather good, but reduced	poor 18%	F_2	—	1926	—

Cross No.	Maternal Species	Paternal Species.	Conjugation of Chromosomes in F_1	Fertility, Seeds per Plant, F_1	Germination	Carried to	Including Backcrosses to	F_1 cultivated Year	Remarks.
18	*nana* n = 24	*arvensis* m = 17	2–6_{II}, 37–29_{I}; occasional one III	250–800, rather good	—	F_1	—	1930	—
19	*Kitaibeliana* n = 18 n = 7	*Kitaibeliana* n = 7 n = 18	abt. 6_{II} + 13_{I}; sometimes one III	ca. 100, very poor	very poor ca. 3%	F_2	—	1929	—
20	*nana* n = 24	*Kitaibeliana* n = 7	5–6_{II}, 21–19_{I}; III + polysomes occur	250–300, not poor	—	F_1	—	1930	—
21	*nana* n = 24	*lutea* n = 24	15–18_{I}; polysomic conjugation	50–300, rather poor	—	F_1	—	1930	—
22	*lutea* n = 24	*Battandierii* n = 26–30	—	50–100 not good	50%	F_2	—	1923	—
23	*Battandierii* n = 26–30	*calcarata* n = 20	—	16–60, poor	poor	F_2	—	1929	—
24	Cross 7, F_1 n = 13 × 11, 10	Cross 1, F_1 n = 11 × 10	—	33–325, variable	variable	F_2	—	1928	quadruple hybrid
25	Cross 7, F_1 n = 13 × 11, 10	Cross 1, F_1 n = 24 × 26–30	—	130–150	poor	F_2	—	1928	quadruple hybrid

high chromosome numbers and species with low chromosome numbers (hybrids, numbers 3, 12 and 15). In these cases, more bivalents are formed than expected from the number of chromosomes in the species with the low chromosome number (*cf. Papaver*, p. 221). It is interesting to note that in three crosses (numbers 7, 11 and 18) the hybrids showed least pairing between chromosomes although the chromosome numbers of the species are comparatively high. From these cytological observations it is possible to estimate the chromosome relationships of the different species. It is seen, for example, that the hybrids involving *elegantula* ($2n = 20$), *rothomagensis* ($2n = 34$), or *lutea* ($2n = 48$), probably contain most multiple associations of chromosomes while the chromosomes of *nana* ($2n = 48$) are not capable of autosyndesis in a species hybrid.

A cogent scheme for the chromosome constitution of the species can be formulated.

diploid, *AA*	*V. Kitaibeliana*	$2n=14$
tetraploid, *AABB*	*V. tricolor*, *V. alpestris*	$2n=26$
hexaploid, *AABBCC*	*V. arvensis*, *V. rothomagensis*	$2n=34$
	V. Kitaibeliana	$2n=36$
octoploid, *AABBCCCC*	*V. nana*, *V. lutea*	$2n=48$

In the above scheme each letter represents a set of six chromosomes. It will be noticed that there is no constant basic number x of the sub-genus, nevertheless, the forms with the haploid numbers 7, 13, 17 and 24 appear to bear some resemblance to a group with the haploid series 6, 12 and 18. Possibly the change from the euploid to the aneuploid series is directly responsible for the various specific differences that have been noted between the forms. The change in balance by the addition of a chromosome probably derived by duplication, would create a morphological and physiological change sufficient to isolate the new form from the old, in the wild state. The change in chromosome content in an additive manner is apparently common in this sub-genus and it occurs even in one species.

V. Kitaibeliana, to which group *V. nana* belongs, is an instructive example of evolutionary change. The species is known in two forms ($2n = 14$) and ($2n = 36$), which are morphologically very similar although their chromosome numbers do not conform to a geometrical series. Further, hybrids between them show as much if not more, failure of chromosome pairing as do hybrids between taxonomic species. The form *nana* is more compatible with the *arvensis* group than with its own *Kitaibeliana* group.

On cytological grounds alone one is able to say that these various species are related closely to one another and that they have evolved by segmental interchange, polyploidy and hybridisation as in other genera. The evolutionary processes of *Viola* are in contrast to those of *Nicotiana* due to the fact that the aneuploid condition is more viable in *Viola* than in *Nicotiana*. *Crepis* probably occupies an intermediate position in this respect.

The genetical study of *Viola* fully confirms, and also extends, the conclusions derived from the cytological study of the forms. Much painstaking work has been done by Clausen in identifying the various factors involved in the inheritance of flower colour, anthocyanin distribution, shape and size of flower, presence and absence of labellum, and length of life. These factors may be transferred from one species to another by hybridisation and an extraordinary range of phenotypes can be produced. Characters such as labellum and size of flower, which systematists justly use for classification, are inherited in a similar way to varietal differences. As expected from the cytological constitutions, polymeric factors are common in the group. This is especially the case in regard to the factors controlling anthocyanin production. Other factors, however, are sometimes not duplicated. " Addition, subtraction, duplication and exchange of entire chromosomes or parts of them may account for many deviations from an identical behaviour by chromosomes of species with the same chromosome number." (Clausen, 1931*a*, p. 300).

The taxonomic criteria of morphological difference and intersterility for species delimitation are certainly difficult to maintain in view of the experiments on *Viola*. Phylogeny may not be appealed to, since the phylogeny of the *Melanium* violets is probably similar to a network rather than to a branching tree.

The manner of evolution of some species in this section has probably been repeated in the production of the species *V. phænoelegantula*, *V. crassicaulis*, *V. hyperchromatica* and *V. velutin*, which are forms that have only arisen from species hybrids in culture. The first has 25-27 chromosomes, and arose from *V. tricolor alba* ($2n = 26$) × *V. elegantula* ($2n = 20$). The second has 25-26 chromosomes, and arose in the F_2 from *V. tricolor alba* ($2n = 26$) × *V. Orphanidis* ($2n = 22$). *V. hyperchromatica* ($2n = 42$) arose from the cross *V. tricolor* ($2n = 26$) × *V. arvensis* ($2n = 34$). The increased number of chromosomes resulted from partial doubling of chromosomes during meiosis in the F_1 plant. These forms are very fertile and constant for distinctive characters, but variable in others, although their chromosome numbers range round the numbers given above. (Clausen (1931*b*) has found that plants of *Viola canina L.*, from different districts, have varying chromosome numbers.) See also Fothergill (1938), *Genetica*.

Antirrhinum. The genus *Antirrhinum* may be considered as a contrast to the genera *Crepis, Nicotiana* and *Viola,* which contain species whose evolution is bound up with chromosomal change either in number or structure.

Antirrhinum contains at least eight species (Baur, 1910, 1924), and innumerable wild and cultivated varieties. These species, with the exception of *A. siculum,* cross readily and produce fertile progeny. *A. siculum* produces partially sterile progeny on hybridisation with other species of the same genus. Baur (1924) and Lotsy (1913) have investgiated the progeny of several species crosses. The reciprocal crosses between *A. majus* and *A. glutinosum* (molle) give rise to F_1 hybrids which are similar and intermediate between the parent species in morphology. The F_2 generation exhibits extraordinary variation ; nearly every character is found to vary and to be combined in innumerable ways with other characters. Further, the range in variability of the F_2 exceeds that of the parental species. Teratological flower types which sometimes resemble the flowers of other genera of the *Scrophulariaceæ* are not uncommon.

The cytological behaviour of these hybrids is unknown, but the parental species have sixteen somatic chromosomes. Since the F_1 hybrids are fertile and produce a great range of types in the F_2, it is probable that the chromosomes of the F_1 pair as bivalents, and that the factors are able to cross-over as in the parental species, thus giving rise to great variation.

Nicotiana Langsdorffi, N. alata and *N. forgetiana* behave similarly to the *Antirrhinum* species. Doubts are sometimes raised as to whether specific rank should be given to such a group of plants which do not normally cross, but appear to have homologous parts of chromosomes and allelomorphic factors. On this point Lotsy (1916) and Jordan (1905) have attempted to show that the genotype (biotype) is the basic unit which should have specific rank. While the genotype is certainly a basic unit, it does seem that the *Linnæan* species, which is composed of several biotypes, has a definite recognisable position as a biological unit.

CHAPTER XI

CONCLUSIONS

A SURVEY of the recent results of plant genetics indicates several new lines of work the importance of which was not fully realised a few years ago. The full effect of the study of polyploidy, structural changes, somatic crossing-over, position effect and the physiological actions of the genes is not yet apparent but the influence of this work has already produced disturbing changes in genetical theory. The discoveries of cytology have firmly established the mechanism of inheritance, and have raised many problems which genetics alone can solve (see p. 97). The recent combined genetical and cytological work of McClintock (*Zea*), Belling and Blakeslee (*Datura*), Muller, Dobzhansky, Sturtevant, Beadle, Stern and Bridges (*Drosophila*) provides much valuable evidence in support of the various theories of genetics and cytology. It is possible for example, to follow by genetical means the conditions of chromosome pairing, chiasma formation and disjunction. It is also possible to relate the position of the centromere and trabants to the locus of the genes, while Sturtevant's great work in precisely defining the consequences of the chromosome theory is being directed to include " Position effect " and preferential segregation. Both these last subjects are in their infancy and will probably expand rapidly in the future.

By a combination of genetical, statistical and cytological methods Weinstein, Schweitzer, Charles and Mather show how a precise mathematical determination of genetical phenomena may be made with considerable advantage in practical analysis and also in formulating laws of segregation and chiasma formation (see p. 89).

The prevalence of polyploidy among plants, and its rarity in animals, tended to separate animal from plant genetics, but the study of structural hybridity has counteracted this tendency. Indeed, despite the specialised terminology of each branch of genetics it is essential that the worker on one organism should be aware of the results from other organisms. Plant genetics has shown that Weismann's conception of the isolation of the germ-plasm from the soma is untenable, that the gamete need not be pure for one factor, but may contain more than one allelomorph, even in normal forms, that the pure line theory of Johannsen is valuable in counteracting erroneous views of the action of selection, but is untenable in practical genetics. Animal genetics has shown how prevalent are large and small structural changes in the chromosomes of an organism, how the chromosome theory of heredity may be tested and how the behaviour of the chromosomes may be followed by genetical analysis. In conjunction, plant and animal genetics provide a coherent picture of the hereditary constitution of the individual organism. No longer may the geneticist be charged with solely studying characters which have little or no relation to the vitality of the organisms in the wild. Genes controlling the alternation of generations in the fern (Andersson-Kottö), vitamin content (Crane and Zilva, Sansome and Zilva), Anthocyanin metabolism (Lawrence and Scott-Moncrieff), catalase activity (Overbeek, 1935, 1938), manufacture of chlorophyll, germination of seeds, pairing of chromosomes, sterility, and brittleness of plant to the extent that the plant falls to bits when touched (*Zea*), are shown to behave in inheritance in a similar way to the original green-yellow, round-wrinkled unit characters of Mendel.

A start is now being made (Ephrussi, Scott-Moncrieff, Wit, Blakeslee, 1921) to discover the intervening steps between the gene's action in the cell and the final character expression. It must be emphasised that no geneticist assumes that one gene determines one character in a manner similar to that imagined in the old homunculus theory. Bridges introduced the useful idea of the production of a master substance by a gene. This master substance is supposed to interact with master substances produced by other genes to develop, through a long chain of processes, the final character. The study of the interaction of master substances is obviously the field of physiologists and biochemists. In plants very little is known on this subject, but organiser and inductor substances, hormones and pigment development in animals are slightly better understood. It should be noted that at present no assumptions as to the nature of the gene can be made from its observable effects. The size of the gene (see p. 137) can be estimated and theories as to its chemical and physical nature (Wrinch) can be formulated. Whether the gene exists as a distinctive entity, or is only a particular arrangement of molecules in relation to other molecules is for the future to determine (see Goldschmidt, Wrinch, Winkler).

Gene action and balance can be seen in the diploid, but attention is more sharply drawn to them when polyploids and structural hybrids are considered. The pod structure of *Raphanus-Brassica*, the chromosomal mutants of *Datura*, Tomato, *Matthiola* and *Drosophila* illustrate well the general influence and importance of a stable balance in the life of a plant. It should be noted that different balances of genes in a species lead to changes in morphological and physiological characters which are similar in kind and degree to those associated with allelomorphic gene differences. Lethality of gametes or zygotes is often found associated with deficiencies and duplications. No prediction, however, can be made as to the probable effect of any particular change. In *Iris*, *Biscutella*, *Narcissus*, and *Hyacinthus*, aneuploids ranging in chromosome number between $2x$ and $4x$ can occur, whereas in *Lycopersicum*, *Matthiola* and the majority of plants the survival of forms with more than 1 or 2 extra chromosomes is low.

Dominance of one factor over another as seen in the character expression is another phenomenon of balance. On pp. 114–140 were described the various theories on the constitution of the factor. The theories are all in agreement on two points. The first is that the dominant factor produces a more saturated condition of character expression than the recessive in the presence of a given genetic constitution. The second is that the saturation point in character expression may be varied by a change in factors other than the allelomorphs involved.

Particular emphasis is given to these views by the experiments on polyploids. A factor which is completely dominant in a diploid (**A** dominant to **a** in an **Aa** plant) may not attain the same degree of dominance in a tetraploid until in the duplex condition. Either the balance of dominants to recessives in a simplex form (**Aaaa**) is insufficient, or the balance of **A** factors to the quadruple sets of non-allelomorphic factors is disturbed: the saturation point of the character is not reached until more **A** factors are present.

The examples from *Primula sinensis, Dahlia variabilis* and *Funaria hygometrica,* quoted in Chapter VI, are of particular interest in this respect. The increase in the number of dominant allelomorphs of one factor results in an increase in the expression of the character controlled by the factor. When the stage of saturation of the character expression has been reached, little or no effect of addition of further dominant allelomorphs will be noticed. This saturation point is not reached in the case of the factor **B** of *Funaria hygrometrica,* even in the quadruplex condition, but the expression of capsule colour is probably saturated at a point between the duplex and triplex condition of factor **C**.

Although the heterozygous diploid is intermediate between the homozygous dominants and recessives, the recessive allelomorphs to the **B** and **C** factors in *Funaria* appear to have little influence on character expression in the presence of the dominant. Nevertheless the recessive allelomorphs do exert an effect on the expression which is similar in kind but less in degree than the dominants. This is seen in the fact that c_4 and b_4 give rise to character expressions more similar to the appearance of a simplex or even a duplex in a tetraploid than to the corresponding triploid and diploid recessives.

An extremely informative example is that of *Drosophila melanogaster,* where Stern was able to produce the expression of the dominant allelomorph by duplication of the recessive allelomorphs (see p. 189). Further he proved that factors in other chromosomes influenced the degree of expression of these duplicated recessive allelomorphs. The experiments of Lawrence on *Dahlia variabilis* (see p. 190) indicate that, in addition to the interaction of the products of factor action, there must be considered the competition between the factors for materials necessary for their respective products.

He found that the factors **Y** and **I** for production of flavones interfere with the production of anthocyanins by the factors **A** and **B**. **Y** also interferes with the action of **I**. The analysis of various combinations of these factors in the double autotetraploid *Dahlia variabilis* shows that there is an effect proportional to the number of dominant allelomorphs of each factor present.

Dominance and epistasy are the result of the factors interacting with each other, together with the action of environmental factors upon the development of the organism. It will be seen, therefore, that, starting with the analysis of single factors, genetics has built up a coherent scheme which resembles the outlook of workers in other biological fields. The advantage in the genetical method lies in the fact that it has established a unitary basis for the biological standpoint.

The theories of the gene and gene action which have been given in Chapter III show a remarkable similarity to Blackman's law of limiting physiological factors in its modern guise. Indeed, it is possible to summarise many phenomena in this form. Thus the expression of a character is dependent on all the genetic and environmental factors, its degree being limited by the amount of action shown by the least potent of these.

It should always be realised that the direction of the gene action may be interpreted as a negative action. For example, the older "exaggeration" phenomenon (see Mohr, 1923), in which a deficiency of a locus gives rise to a more extreme type from the wild type than the recessive, is interpreted more correctly by modern genetics, as follows; the "wild type" of eye colour depends on more gene master substance than the recessive allelomorphs, which in turn have more than the absence. Further, the dominant need not necessarily produce more master substance than the recessive. For example, some of the Minutes in *Drosophila* probably give less gene action than the + gene.

Following the Darwinian epoch it was thought that selection could continuously change a race by the aggregation of small mutations directly induced by the selection. This conception was a direct result of the effect of the "Origin of Species" and Galton's "Natural Inheritance" upon biological thought. Point was given to this view by the knowledge that selection of the best individuals in a species could improve the varieties of the species. Johannsen, however, showed that selection could only affect genetically heterogeneous varieties and had no effect on homozygous strains. A description of his experiments with beans will be found in Johannsen (1903).

The theory of the pure line is a valuable theoretical conception, showing that selection acting on the phenotype only indirectly affects the genotype. The knowledge of polyploids, structural hybrids and the high frequency of mutations indicts that a pure line probably does not exist in practice. Even a haploid vegetatively propagated will not give rise to a pure line because variation by mutation, by somatic crossing-over, or position effect is very great (see p. 261).

Heterozygous plants may not show their heterozygosity by segregation. For example, triplex (**AAAa**) tetraploids may only give gametes of the constitution **AA** and **Aa**. When complete dominance is present no segregation is observed. In many organisms (*Pharbitis*, Imai (1930*a*), *Papaver*, Philp (1933), *Chorthippus* (Sansome and La Cour)) the character expression of one gene may prevent the detection of the segregation of other genes. Koller (1932) reports that a race of *Drosophila pseudo-obscura* homozygous for a gene shows variation and fluctuation as the result of the heterozygosity of genes which modify the character determined by the homozygous gene. In structural hybrids and also apparently in what were assumed to be structurally homozygous diploids unsuspected heterozygosity may persist for many generations (see Muller, Bridges).

One of the most remarkable and far-reaching discoveries has resulted from the analysis of salivary gland chromosomes. From the work of Muller, Painter, Bridges, Dobzhansky and Sturtevant it has been shown that the chromosomes of normal *Drosophila melanogaster* contain duplications, deficiencies and inversions. Even in individuals, which on previous knowledge were thought to be normal diploids, there probably are many chromosome abnormalities. As Muller (1938) points out, duplications inserted in a chromosome may undergo mutation and give rise to new genes, thus increasing the potential number of genes in an organism. The position effect phenomenon, first definitely established for the Bar-locus of *Drosophila* by Sturtevant, has been shown to occur in other loci than Bar.

Variations produced in this manner, especially in sections of the chromosome which are " blocked " by small inversions from normal crossing-over, *e.g.*, Dichæte in *Drosophila*, provide more than sufficient basis for evolutionary development and may be the method by which genetic changes of Order or Phyla rank have taken place. It has been shown that despite the prevalence of structural changes, large sections of the chromosomes of the genus *Drosophila* are similar in different species. Their cytological appearance may be rather different, but taken largely gene positions and gene properties of chromosome arms correspond remarkably closely. Similarly, within the *Zea-Euchlæna* or *Secale-Triticum-Ægilops* groups the gene structure of the chromosomes shows a stability and uniformity that is remarkable, when structural changes within a species are so prevalent.

It is also probable that " repeats " and similar phenomena may account for the general absence of segregation of specific and generic characters. Although it is possible to change the Family characters of *Lycopersicum* by combining recessives to give a 5-carpelled fruit, compound inflorescence and apetalous flowers, or to change the life cycle of ferns or *Drosophila* by genes, it is perhaps significant that even after X-rays the visible mutations are most frequently not those which taxonomists use in classification. It may be that, as in the case of the many Minutes of *Drosophila*, the fundamental genes which control type are present several times at different loci. Thus sex determination in *Drosophila melanogaster* cannot be limited to any one position on the *X*-chromosome.

A highly important result of the knowledge of structural changes is that it is necessary to regard the conclusions from secondary pairing, from pairing in polyploids, allo- or autosyndesis, and from the karotype analysis of groups of plants with caution. Conclusions as to the affinities of chromosomes, based on observations of pairing, are less certain than hitherto supposed. It does not necessarily follow that in hybrids between species with different chromosome numbers, the univalents represent the chromosomes of the parent with the higher chromosome number. Chromosome analysis is a valuable method of attack on specific relationships, but should not be given too great an emphasis.

Sewell Wright (1921*a*,*b*, 1930, 1931, 1932), Haldane, Waddington, and Fisher among others have considered mathematically the effects of selection, population size, different methods of breeding, and mutation rates on the survival of genes in the population or line. Dobzhansky's " Genetics and the Origin of Species " gives a masterly account of this work relating to wild populations. One of the most interesting conclusions for the biologist is that " even if the environment is homogeneous for all colonies of one species, and selection and mutation rates are the same, and the initial composition of the populations identical, the lapse of time will bring about a differentiation. This differentiation need not be of an adaptive kind. If the population size is small, favourable mutations may actually be lost and evolutionary changes may proceed against the pressure and direction of selection. In large populations, however, selection will act to an amount approximately proportional to its intensity." Whether the effect of mutation is perceivable in a population depends on the three quantities, size of population, intensity of mutation rate and intensity of selection.

THE SPECIES PROBLEM

A general survey of species from the genetical standpoint indicates that the change from one type to that of another is more frequent than was at one time thought. Hybridisation, factor mutation and structural alteration of the chromosomes in combination with polyploidy give great opportunity for variation. The fundamental nature of balance as the limiting factor of the extent to which change can take place is seen by comparison of the manner in which such genera as *Antirrhinum, Crepis, Viola, Nicotiana, Pyrus* and *Drosophila* have evolved. One species may be able to withstand the dropping out of a chromosome, while another may not. The progeny of hybrids between two species may have great variability while others may be relatively constant. A particular example of this difference in hybrids is seen in the contrast between the genetic behaviour of the hybrids *N. Tabacum* × *N. sylvestris* and *N. rustica* × *N. paniculata.* The variability can arise either as the result of genetic variability in the parental species or as the result of allosyndesis and chromosome change in the polyploid derivatives.

The last ten years have seen a considerable change in the attitude expressed in the genetical literature upon the subject of species and their origin. The definition of a species is extremely difficult, and we must still rely upon the working classification of the taxonomists.

Instead of it being easier, it is more difficult to define a species at the present time than before. As Anderson (1928) points out, the delimitation of species of *Iris* differs from that of species of *Aquilegia* (Anderson and Schafer, 1931) primarily because of their different modes of life. In one, the principal means of propagation is vegetative while in the other it is sexual. The primary cytological, genetical and ecological behaviour of the species is even more important in delimiting species than the secondary physiological properties. Huskins pointed out that two species cannot be differentiated on their inability to form fertile F_1 plants as was formerly supposed. On one hand the F_1 hybrid between *Raphanus* and *Brassica* is perfectly fertile. On the other hand, diploid and tetraploid plants of a single species may cross only with difficulty and the F_1 plants so produced are nearly sterile. Indeed, one and the same plant of the tomato may have fertile diploid and tetraploid parts (see p. 163) which are practically inter-sterile. One race of a species may become practically sterile through segregation of a recessive factor which interferes with normal meiosis (Beadle (1930) in maize) or with pollen divisions (Beadle, 1931). Mendelian incompatibility factors in *Nicotiana* and cherries are further examples of sterility.

Gordon (1936), Dubinin *et al.* (1934) (*J. Exp. Biol.*), Timofeeff-Ressovsky, H. A. and N. W. (1927), with *Drosophila* ; Sansome and La Cour with *Chorthippus* and *Melandrium* (Sansome, unpub.), have studied the survival and mutation rates of experimentally bred species after release in the wild. Dobzhansky (1937) (*Drosophila*), Anderson and Sax (1936) (*Tradescantia*), Simonet (1932) (*Iris*), Goodspeed (1933), East (1928, 1935) (*Nicotiana*), Babcock and Navashin (1930), (*Crepis*), Clausen (1931*a*) (*Viola*), Müntzing (1930, 1932, 1932*a,b*, 1938), Marsden-Jones and Turrill (*Centaurea*), Brunn (*Primula*), and many others have shown conclusively that the taxonomic arrangement of species in a genus is, in general, a natural one. Further, cytogenetics and ecology have shown that the taxonomic criteria employed in species classification have a biological foundation and are not altogether arbitrary. Thus the taxonomist has isolated the constant and similar features from the dissimilar and variable features in different groups of individuals—a process which involves field study or its equivalent. These constant features are based on identical or homologous factors in the species of one group (*cf. Viola*, p. 328). Hence the taxonomist has chosen the more actively selected features on which to base his classification and in so doing has analysed the results of genetical and ecological processes.

The nature of these processes is, in our view, unknown. On the one hand, gene and chromosome change is prevalent in any organism either in the wild (*Drosophila*, *Chorthippus*, *Melandrium*, *Viola*) or in cultivation (maize, pear, apples, *Chrysanthemum*). On the other hand analysis shows that old world and new world species of *Crepis*, *Philadelphus*, *Platanus*, *Triticum* and *Ægilops* show a constancy of chromosome and gene structure which is astonishing. The question is not as to how species arise but rather as to how a group of plants or animals remain similar and recognisable as an entity, variety or species.

While phylogenetical relationships based on cytological similarities—karyotypes—have been formulated in the past, it is necessary to reserve judgment on their validity in detail analysis. Greater gross chromosome structural differences can be found within races of *D. melanogaster* than between this species and *D. similans* (Dobzhansky and Tan, 1936). Further, these structural differences were mainly seen from studies on salivary gland chromosomes. Metaphase plates, the usual object of study in plants only reveal the gross differences which we now know are less important than many small differences.

The experiments mentioned above indicate that in order to analyse the more intricate species relationships in those genera which are known to be difficult, and to obtain a better understanding of the status of the species, it is necessary to combine field study with cultural and genetical experiments. An interesting case where from ecological and physiological points of view genetics has aided the elucidation of species relationships is that of Gregor and Sansome (1930) and Gregor (1931) in *Phleum*. The British *Phleum pratense* will not cross with the American *Phleum pratense*, but both will cross with *P. alpinum* from the mountains in Scotland. The forms of habit in the two varieties of *P. pratense* are parallel, and no reasons for separation of the varieties from one another were apparent until an examination of the chromosome complements was made. British *P. pratense* had 14 chromosomes and was diploid, while the American *pratense* had 42 chromosomes and was hexaploid. *P. alpinum* had 28 chromosomes and was tetraploid. Gregor hybridised *P. pratense* ($2n = 14$) with *P. alpinum* ($2n = 28$) and obtained a hybrid with 21 chromosomes. This hybrid gave 4 viable seeds from about 500,000 flowers. These four seeds gave rise to plants with the hexaploid number of chromosomes $2n = 42$, which were cross-fertile with the American variety of *P. pratense*. Hence by outcrossing one variety of *P. pratense* to another species, a hybrid was obtained which was fertile with the other variety of *P. pratense*. It is believed by American botanists that *P. pratense* is not indigenous to America, but was introduced about the seventeenth century from Europe, where *P. alpinum* and *P. pratense* are both found. It may be that these workers have repeated under controlled conditions the process by which the hexaploid American variety was formed in nature. Similar species synthesis is probably that carried out by Müntzing in *Galeopsis*, where a form similar to *G. Tetrahit* was produced by hybridisation.

Genera such as *Crepis, Galeopsis, Phleum, Primula, Digitalis, Spartina, Nicotiana, Delphinium* have furnished examples of the origin of new forms strictly delimited from the original parents. How these forms are established as ecological units is for the future to determine. The flora of Australia is of great interest in this respect, according to the late Professor A. A. Lawson. Here the endemic flora consists of well-defined isolated species, while the incursive flora is hybridising and giving rise to many new types, which are gradually driving the endemic plants to more restricted habitats.

An insight into the methods by which species are delimited one from another by natural selection has also come with the accumulation of knowledge as to the manner of origin of species. From a study of these methods of delimitation it should be possible to obtain criteria for the natural classification of species. A species is produced and remains constant as a distinct form under the strict control of natural selection which acts not as a creative agent but as a choosing agent.

The main processes in the evolution of a species are (1) creation of material on which selection may act; (2) isolation by geographical or physiological causes from related species; (3) selection of characters necessary for survival under the requirements of the habitat in which the plant is placed. The first two processes do not require further attention at this point; they are dependent upon the genetical and cytological background of the species. The third process is one of environmental selection of the available characters provided by the first process. Naturally, the possibility of obtaining the ideal form to suit the environment depends on the results of process (1)—the production of new and heterogeneous material by quantitative or qualitative change. Ecology is the study of the third process.

The importance of combined genetical, ecological and taxonomic work cannot be over-emphasised. Attempts have been made by various workers (Bonnier, Massert, Warming and Clements) to study the life of plants in their natural environments and under diverse conditions. Insufficient attention to the heritable constitution of the plants involved, however, impairs the value of their work. It is only by observing the reactions of a particular genetic constitution to different environments that the agents of natural selection and physiological isolation may be identified. Without the knowledge of the genetic constitution, variability of more than one plant of any species cannot be attributed to environmental influence alone. Turesson (1921-1931) in Sweden, Marsden-Jones and Turrill (1930), and Gregor (1930, 1931) in Britain, and Anderson (1928) in America, are the pioneers in this combined ecological and genetical work termed genecology by Turesson (*cf.* Barton-Wright, 1932). Valuable work on interspersing known races of one species in different environments is being done in Russia by Sukatschew (1928) and Dubinin.

The following discussion of Turesson's work (1922, 1923) will indicate that taxonomic species (*linneons*) have a natural constancy and status which does not justify their abolition as natural units. Turesson transferred individuals of a number of plant species from various localities in Sweden to the common environment of the experimental garden. Observations were made on the changes brought about during at least two years' culture upon the morphology of the individuals, and breeding methods were used to show the genetic constitutions of the plants concerned. Wherever a different ecological type of environment occurred, such as cliffs, dunes, etc., along the coast of Sweden it was found that there was a genetically distinct variety of the species which was suitable for the environment. For example, the zone between the cliff and dune regions contained a population of plants consisting of individuals of the neighbouring regions together with hybrids between them. Seeds and plants of species, such as *Hieracium umbellatum, Centaurea jacobea, Atriplex spp.* and many others were collected and studied in culture. It was found that the distinct characteristics of a population from the different ecological habitats retained their distinguishing features to such an extent that Turesson could say, by examination of the plant, from which district and which habitat it came. In many cases these characteristics were shown to be inherited. When hybrids were made between two plants from different habitats the heterogeneity of the progeny resembled that of the wild population found in the intermediate zones between two definite ecological habitats.

It was sometimes found that the characteristics of the population from one extreme habitat were accentuated under cultivation (breadth of leaf in *Hieracium umbellatum*), while in others the population that appeared uniformly dwarf in the wild varied in heritable habit and height differences when under culture. The explanation, of course, is that the response of a certain genetic constitution to the selective action of environment is different in different plants. A factor for dwarfness and its allelomorph for tallness may not have a great range in character expression in one species, while in another species the variability of the .expression may be great. Hence, in the first case, selection of the phenotype will adversely affect one factor, while in the second case, where the phenotypic range of one genotype is great, the differential selection between two factors will be less intense.

The attempt, however, to interpret the correspondence between habitat and habitat-type of the inhabitants as an adaptational process must be carefully analysed in order to avoid too great a generalisation. It is evidently the genotypical constitution of the plant which determines its survival in any habitat. In what manner does a suitable genotype come to be present in a particular habitat for which it is entirely suitable ? For example, the prostrate form of *Hieracium umbellatum,* which is found on the stationary beaches, is not found on the neighbouring moving dunes where it is replaced by a form with much stronger shoot regeneration (probably being more able to resist being covered by moving sand). It is not necessary in this book to give further evidence that the environment does not directly create suitable characters (inheritance of acquired characters).

In some parts of Sweden the dune type of plant is not present, although the less specialised inland form is present, while in other districts the dune type is found. Evidence from plants gathered from several different habitats in one region of Sweden indicates that they are related to one another since they possess several characters in common, such as leaf shape, which are not of primary ecological importance.

Thus we are driven to the conclusion that varieties suitable for survival in an extreme habitat are selected out of the population of the immediate undifferentiated regions.

The population of a cliff in one district has descended from the population of inland plants in the neighbourhood and has not migrated from a cliff in a different district. This view is entirely opposed to the well-known migration theory but is closely similar to an older theory of polygenesis and can be extended to many examples of geographic distribution. As a result of this analysis of wild populations the *linneon* has been split up into smaller ecological units, each based on genetical considerations. These units in many cases may correspond to the biotypes of Jordan (1905), or the Hagedoorns (1921). Nevertheless we feel, as Turesson does, that to limit the term " species " to such biotype units is to strip the species *linneon* of its characteristic quality, that of being able to react genotypically to a wide range of ecological requirements without losing its general common morphology.

The discovery of the biotype or separate genotype has provided a basic unit from which to build up a composite structure, the *linneon*, but it has not destroyed the value of the *Linnæan* species. We are therefore of the opinion that a real biological basis founded on the combined use of ecology and cytogenetics can be provided for the species of the taxonomists. Indeed, the most recent work in genetics has shown that the *Linnæan* species is a more fundamental unit than shown by its external characters, its chromosome structure or gene content. In other words, the evidence from taxonomy, palæobotany, morphology, cytology and genetics agrees in establishing species and higher groups in a natural relationship. But it would appear that although genetics can proceed further in the analysis than other branches, the nature of the stability of the species as a genecological entity is still unknown. Possibly the key to the situation is the unknown actions of natural selection. It is essential that more experimental work of the type begun by Dubinin and his co-workers, Babcock, Gordon, Sansome and La Cour, Nabours and Philip, must be done to discover how far our theories regarding selection are sound.

KEY TO LITERATURE

Résumés

Ægilops and Triticum, Sorokina (1934), *Bull. A. Bot.*, II., 6 Crossing-over, Eloff (1932), *Genetica*, Mather (1938), *Bio. Rev.* Eversporting Varieties, Roelof (1937), *Genetica*. Fatuoids, Aamodt *et al.* (1934), *Canad. J. Res.* Heterothallism, Quintanilla, *Res. Bull. Univ. Coimbra*. Incompatibility, Sears (1937), *Genetics*. Pollen, Brink (1924), Branscheidt (1930), *Z.I.A.V.* Sex, Breslavetz (1934), *Bull. A. Bot.*, II., 6. Correns (1928), *Handb. Vererbungswiss.* 2. Variegation, Chittenden (1927). Plasmatic Inheritance, Sirks (1938), *Bot. Rev.* 4, 113–131. Polymerism, Tjebbes (1931), *Biblio. Genetica*. Unstable Genes, Demerec (1935), *Bot. Reviews*. Genetics and Species, Harland (1936), *Biol. Reviews*, Dobzhansky (1938).

Genes

Gene mutation

X-rays. Buchholz and Blakeslee (1936) Huskins and Hunter (1935), *P.R. Soc.* Husted (1936). Levitsky and Araratin (1931). Marshall (1935). Mather (1934). Mather and Stone (1933), *Cytologia*. Mather and Stone (1933), *J. G.* Muller, (1934), *Science of Radiology*. Nebel (1936). Patterson (1929–1930). Patterson and Suche (1934). Stadler (1930), *J. Hered.* (1931), *Sci. Agri.* Stubbe (1935), *Z.I.A.V.* Timofeeff-Ressovsky (1930), *Biol. Rev.* White (1935), *P.R. Soc.*

Action of Genes

Affecting gene mutation

Demerec (1937), *Genetics*. Muller (1928), *Genetics*. Sturtevant (1934), *Quart. Rev. Biol.*

Influencing meiosis

Crepis, Richardson (1935), *J. G.* *Datura*, Blakeslee (1928), Carn. Inst. *Lolium*, Peto (1934), *J. G.* *Matthiola*, Lesley and Frost (1927). *Nicotiana*, Clausen (1931), *Amer. Nat.* *Rumex*, Yamamoto (1931), Bot. and Zool. *Secale*, Lamm (1936), *Hereditas*. *Sorghum*, Huskins and Smith (1934), *J. G.* *Triticum*, Sapehin (1933), *Bull. App. Bot.* *Viola*, Clausen (1930, 1931), *Hereditas*. *Zea*, Beadle and McClintock (1933), *Cytologia*. Beadle (1933), Bergner, Cartledge and Blakeslee (1934), *Cytologia*. Darlington (1934), McClintock (1929), Randolph (1928).

Genes for Sterility

Datura, Bergner, Cartledge and Blakeslee (1934), Buchholz and Blakeslee (1936), *Genetics*. Oats, Wheat, Huskins and Hearne (1933). *Sorghum*, Huskins and Smith (1934). *Pisum*, Koller (1938), Sansome (unpub.). *Lathyrus*, Fabergé (1937). *Zea*, Beadle (1930–1933).

Gene, Structure or Environment affecting Crossing-over

Drosophila, Dobzhansky (1924–1935), Friesen (1934), Patterson and Suche (1934), Sturtevant (1917, 1926). *Chorthippus*, White (1934), *J. G.* *Primula*, Gregory, de Winton and Bateson (1923). *Vicia, Tradescantia,* Sax (1935), *Cytologia. Zea,* Collins (1937), *U.S. Dep. Bull.* 1468 ; Emerson and Hutchinson (1921), *Genetics* ; Rhoades (1936) ; Stadler (1926), *Genetics* ; Straub (1937), *Br. D. Bot. Gdns.* 193, *Zeit. Bot.*

Mutations due to Age or Heat

Hordeum, Peto (1933, 1937), *Canad. J. Res. Crepis,* Navashin (1930).

Mutating Genes

(See Demerec, Eyster, Rhoades, Anderson, Emerson).

Mirabilis, Showalter (1937), *Abstr. Genetics. Nicotiana,* Kostoff (1935). *Petunia,* Malinowski (1935), *Genetics. Primula,* de Winton and Haldane (1935), p. 15. *Portulaca,* Imai and Kanna (1935), *Genetica.*

Mutable genes. Demerec (1935), *Bot. Rev.* Demerec (1937), *Genetics* (*Drosophila*). Demerec and Slizinski (1937), (*Drosophila*). Goldschmidt (1938), *Physiological Genetics* (McGraw Hill). Imai (1934), *J. Coll. Tokyo. Agri.* (*Pharbitis*). Kihara (1932), *Agric. Hort.* (*Celosia*). Plough and Holthausen (1937), *Am. Nat.* Rhoades (1938). Stern (1935), *P.N.A.S.*

Mutations

Temperature. Plough and Ives (1935), *Genetics.* Timofeeff-Ressovsky (1934), *Biol. Rev.* Jollos (1934), *Genetica.* **Frequency.** Berg (1937), *Genetics.* Sturtevant (1937), *Biol. Rev.*. Gowen and Gay (1933). Demerec (1937), *Cytologia.*

Linkage

Calculation. Immer (1930). Mather (1938), Methuen. De Winton and Haldane (1935). **Maps and groups.** *Drosophila melanogaster* (p. 98). *D. pseudoobscura,* Tan (1936), *Genetics* ; (1937), *J. G.* ; Crew and Lamy (1935), *J. G.*; *Lathyrus,* Punnett (1927). *Lycopersicum,* MacArthur (1934). *Pharbitis,* Imai (1929, 1931). *Pisum sativum,* Winge (1936), *Trav. Carlsberg Lab. Primula sinensis,* de Winton and Haldane (1935). *Zea,* Emerson, Beadle and Fraser (1935).

Time of Division of Chromosome

Darlington (1935), *Proc. Roy. Soc.* 118. Goodspeed, Uber and Avery (1935), *Univ. Calif. Publ.* 18. Huskins (1932), *Trans. Roy. Soc. Can.* Huskins and Smith (1935, 1934), *J. G.* Kuwada and Nakamura (1935), *Cytologia.* Nebel (1932), *Zeit. f. Zell. Mikr. Anat.* Ruttle and Nebel (1937), *Cytologia.* Sax and Sax (1935), *J. Arn. Arb.* Stebbins (1935), *Am. Nat.* Dermen (1936), *J. Arnold. Arbor.*. McClintock (1938).

Chromosome Structure

Huskins (1937), *Cytologia.* Kuwada (1938), *Cytologia.* Matsuura (1938), *Cytologia.* Sax (1936), *Genetics.* Wrinch (1936), *Protoplasma.*

Nucleolus and Constrictions

Beadle (1933) *Cytologia* (*Zea*). Chen (1936), *P.N.A.S.* (Protozoa). Fernandes (1936), *Bol. Soc. Broterium* (*Narcissus*). Heitz (1931), *Planta.* Lesley and Lesley (1935) (*Lycopersicum*). Levan (1936), *Hereditas* (*Allium*). Matsuura (1938), *Cytologia* (*Trillium*). McClintock (1934), *Z. Zell. u. Anat.* (*Zea*), Richardson (1935), (*Crepis*). Smith (1933), *Am. J. Bot.*

Crossing-over

Method of

Drosophila, Anderson (1935) ; Beadle (1935) (attached *X*), *Genetics* ; Beadle and Emerson (1935), *Genetics*. *Zea*, Brink and Cooper (1935), Creighton and McClintock (1931), McClintock (1931), Rhoades (1935). **Mathematics.** Charles (1936), *J. G.* ; Mather (1937) ; Schweitzer (1935), *Genetics* ; Steinberg (1935), *Genetics*.

Somatic. Peto (1935), Stern (1936), Jones (1938), *P.N.A.S.* **In male *Drosophila*.** Friesen (1934), *Biol. Zentral.* ; Kikkawa (1933), *Proc. Nat. Acad. Tokio* ; Moriwaka (1935), *Proc. Nat. Acad. Tokio* ; Philip (1935), *J. G.* ; Whittinghill (1937), *Genetics*. **In female *Drosophila*.** Whittinghill (1938), *Genetics, Abstract*.

Cytological results of Crossing-over

Zea, McClintock (1931*a*, 1933, 1938) (see pp. 88, 254). *Trillium*, Smith (1935), *J. G.* *Lilium* (Richardson (1936), *J. G.*

Crossing-over at pre-meiotic divisions or in somatic tissue

Friesen (1936). Muller (1916), *Am. Nat.* Patterson and Suche (1934), *Am. Nat.* Shull and Whittinghill (1934), *Science*. Stern (1938), *Genetics*. Whittinghill (1937). Philip (1935), *J. G.* See also Ring Chromosomes.

Chromatid Segregation

Datura, Blakeslee and Avery (1934). *Dahlia*, Lawrence (1931). *Lycopersicum*, Sansome (1933), Lesley (1937). *Primula sinensis*, de Winton and Haldane (1935). *Rubus*, Crane and Darlington (1932). *Zea*, Rhoades (1933).

Salivary Gland Chromosomes in Genetics

Bridges (1938), *J. Hered.* Dobzhansky and Sturtevant (1934). Koller (1936), *J. G.* Dobzhansky and Tan (1936), *Z.I.A.V.* Mackensen (1935), *J. Hered.* Painter (1935), *Genetics*. Tan (1935), *Genetics*.

Structural Changes

Allium, Levan (1936), *Hereditas* ; Emsweller and Jones (1938), *Bot. Gaz.* *Avena*, Philp (1933, 1938). *Briza*, Kattermann (1938), *Planta*. *Brodiæa*, Smith (1933), *P.N.A.S.* *Campanula*, Gairdner and Darlington (1931). *Crepis*, Müntzing, A. (1934). *Datura*, Belling, Blakeslee, Satina, Avery (1925–1938). *Drosophila*, Dobzhansky (1929–1932, 1934, 1937), *J. G.* ; Dobzhansky and Dobzhansky (1933) (" Bobbed "). Dobzhansky and Tan (1936), *Z.I.A.V.* ; Friesen, H. (1935) ; Hoover (1938), *Z.I.A.V.* ; Gershensen (1933) (inert regions) ; Painter (1934), *Genetics* ; Koller (1936), *J. G.* ; Offermann (1936) (branched chromosomes) ; Patterson, Wilson and Bedischek (1935), *Genetics*. *Godetia*, Håkanssen (1925, 1931), *Hereditas*. *Œnothera*, see pp. 264-296. *Matthiola*, Philp and Huskins (1931), Armstrong and Huskins (1934) *Petunia*, Malinowski (1935), *Genetics*. *Pisum*, Håkanssen (1936) ; Nilsson, E. (1935), *Hereditas*, 21 ; Sansome (1929, 1932, 1933, 1938, and in press) ; Sutton (1935), *Ann. Bot.* *Polemonium*, Clausen (1931), *Hereditas*. *Rhoeo discolor*, Darlington (1929). *Tradescantia spp.*, Darlington (1929), Anderson and Sax (1936). *Trillium*, Smith (1935), *J. G.* *Triticum*, Smith (1936), *Am. Nat.*, abs. ; Ellison (1938), *J. G.* *Tulipa*, Upcott and La Cour (1936), *J. G.* *Zea*, Anderson and Clokey (1934), *Am. Nat.* ; Burnham (1930) ; Brink and Cooper (1932) ; Emerson (1921, 1924) ; Randolph (1932) (from heat) ; Rhoades (1933*a*, *b*), McClintock (1930, 1931, 1933, 1938). *Zebrina pendula*, Darlington (1929).

Deficiencies and Duplications (genetically analysed)

Drosophila, " White," Mohr (1923). " Yellow achæte," Muller (1935), *J. Hered*; Demerec and Hoover (1936), *J. Hered.*; Stern (1935), *P.N.A.S.* " Scute," Sturtevant and Beadle (1936), *Genetics.* " Roughest," Emmens (1937), *J. G.* " Facet," Oliver (1937), *Am. Nat.*

Zea, Stadler (1935), McClintock (1933, 1938).

Inversions

Drosophila pseudoobscura, Dobzhansky and Sturtevant (1938), Grüneberg (1935, 1937), Hoover (1938), *Z.I.A.V.*; Steinberg (1936), Sturtevant and Beadle (1935). *Fritillaria*, (Frankel (1937), *Vicia*, Mather (1934). *Zea* McClintock (1931, 1933). *Lilium*, Richardson (1936), *J. G.* *Trillium*, Smith (1935). *Tulipa*, Stone (1933), Upcott (1937), *J. G.* *Crepis*, Müntzing (1934).

Ring Chromosomes

Crepis, Navashin (1930), *Univ. Calif. Pub. Agri. Soc.*, 6. *Drosophila*, Morgan, L. V. (1933), *Genetics.* *Pisum*, Atabekowa (1936), *J. Biol. U.S.S.R.* *Tradescantia*, Husted (1936), *Genetics.* *Trillium*, Huskins and Hunter (1935), *Proc. Roy. Soc. Gr. Br.* *Tulipa*, Upcott (1937), *J. G.* *Zea*, McClintock (1932, 1933, 1938), McClintock and Rhoades (1932).

Pairing in structural heterozygotes

Dobzhansky (1931, 1933*a*, 1934*a*). Beadle (1931), Dobzhansky (1936), Kozhenikov (1936), McClintock (1931, 1933), Darlington (1937).

Polyploidy

Origin of

In a race (maize), Avdulov (1935), *Bull. Appl. Bot. and Gen.* II. *Acer* (3), Meurman (1933). Banana (3), (4), Cheesman (1932). From twin seedlings, Müntzing (1937), *Cytologia.* *Populus, Müntzing* (1936), *Hereditas.* *Potentilla*, Müntzing (1931), *Hereditas.* *Rumex*, Ono (1935).

Colchicine

Blakeslee and Avery (1937), Dermen, *J. Hered.* (1938); Demerec (1938), *J. Hered*; Levan (1938), *Hereditas*; Nebel and Ruttle (1938).

Heat

Barley, Müntzing, Tometorp and Mundt-Petersen (1936), *Hereditas.* Maize, Randolph (1932, 1935), Wheat, Dorsey (1936), *J. Hered.* *Rhoeo*, Sax (1936), *J. Arn. Arb.*

Size

Cultivated Autopolyploids

See Müntzing (1933, 1936).

Citrus, Frost (1926) (lower vigour). *Crepis*, Navashin (1929). *Zea*, Eyster (1934), Randolph (1935). Pineapple, Collins and Kerns (1935). Rice, Ramiah Parthasarthy and Ramanujam (1935), *Proc. Ind. Acad. Sci.*

Wild Autopolyploids

Crocus, Kararava (1932). *Populus*, Müntzing (1936), *Hereditas.* *Thea*, Kararava (1932). *Tradescantia*, Anderson and Sax (1936). Rice, Ramiah, Parthasarathy and Ramanujam (1935), *Proc. Ind. Acad. Sci.*

Autopolyploids.

Physiology.

Lycopersicum, Fabergé (1936) (growth and variability). Apples, plums, pears, Crane (1936) (longer juvenile period). *Citrus*, Frost (1926) (slow to flower). *Tradescantia*, Anderson and Sax (1936) (longer flowering period).

Distribution in wild

Hagerup (1928), Tischler (1935), Müntzing (1936). *Solanum*, *Brassica*, Schlosser (1935) (less winter-hardy and lower osmotic pressure); Karpechencko *et al* (1935), *Bull. App. Bot. U.S.S.R.*

Syndiploidy

Acer, Meurman (1933). *Anthoxanthum odoratum* (4), Kattermann (1931). *Chrysanthemum ornatum*, Shimotomai (1931). *Kniphofia*, Moffett (1932). *Crepis tectorum*, Navashin (1926) (500 chromosomes in one cell). *Crepis* haploid, Hollingshead (1930). *Datura* haploid, Blakeslee and Avery (1937). *Lycopersicum esculentum*, Lindstrom and Koos (1931) (Haploid). *Nicotiana* haploid, Ruttle (1928). *Prunus avium*, Darlington (1930). *Raphanus-Brassica*, Karpechencko (1937). *Triticum* × *Ægilops*, Kihara and Lilienfeldt (1934). *Zea*, McClintock (1929) (pollen), Beadle (1933).

Output of Triploids

Allium, Levan (1936), *Hereditas*; McClintock (1929). *Datura*, Satina and Blakeslee (1937). *Hemerocallis*, Dark (1932), *New Phyt.* *Hyacinthus*, Stone and Mather (1932). *Lycopersicum*, Lesley (1926). *Narcissus*, Nagao (1935), *Jap. J. Genetics.* *Petunia*, Dermen (1931), *Am. J. Bot.*. *Scilla*, *Tradescantia*, Darlington (1926, 1929). *Solanum*, Müntzing (1933), *Hereditas.* *Tulipa*, Darlington and Mather (1932).

Monosomics

Aneuploids

Wheat, Avery (1929); Clausen (1931), *Am. Nat.* Nishiyama (1933), *Jap. J. Genetics*; Powers (1932), *J. Agr. Res.*; *Nicotiana*, Clausen and Goodspeed (1926); Goodspeed and Avery (1933), *Genetics*; Håkansson (1932), *Hereditas*; Lammerts (1932); Olmo (1935).

Haploids

From heat. Randolph (1932). *Crepis*, Hollingshead (1930), *Univ. Calif. Pub.* *Datura*, Satina, Blakeslee and Avery (1937). *Linum*, Kappert (1933), *Biol. Zent.* *Gossypium*, Harland (1936), *J. Hered.*

Twin Seedlings

Haploids. Cotton, Harland (1936), *J. Hered.*. Flax, Kappert (1933), *Biol. Zentral.* *Datura*, Satina, Blakeslee and Avery (1937).

Polyploids. Gramineæ. Müntzing (1937), *Cytologia.*

Heterosis

Ashby (1930–1935), *Ann. Bot.* Powers (1935). Sax (1923). Sirks (1925, 1932), *Genetica.* Wexelsen (1934). Luckwill (1938), *Ann. Bot.* East (1937), *Genetics.*

Incompatibility

Stout (1938), *Bot. Rev.*; Sears (1937), *Genetics*; Anderson and de Winton

(1935). *Antirrhinum*, Brieger (1935), *J. G.*; Gruber and Waldenburg (1937), *Z.I.A.V.* *Nicotiana*, Brieger (1935), *J. G.* *Œnothera*, Emerson (1938), *Genetics*. *Brassica*, Alam (1936), *J. G.* *Petunia*, Wergin (1936), *Z.I.A.V.* *Reseda*, Eigsti (1937), *Abstr. Genetics*. *Capsella*, Riley (1936), *Genetics*.

Species Relationship

Aquilegia, Anderson and Schafer (1931). *Crepis*, Avery (1930), Babcock (1930–1936), Babcock and Navashin (1930), Babcock and Cameron (1934), Babcock and Emsweller (1936), Babcock and Cave (1938), *Z.I.A.V.*; Navashin (1931). *Dahlia*, Lawrence. *Drosophila*, Dobzhansky (1935); Dobzhansky and Tan (1936), *Z.I.A.V.*; Dobzhansky and Beadle (1936), *Genetics*; Dobzhansky and Sturtevant (1936); Sturtevant and Tan (1937), *J. G.*; Tan (1936), *Z.I.A.V.* *Nicotiana*, East (1937), *Genetics*. *Secale-Triticum*, Aase (1930). *Tradescantia*, Anderson and Sax (1936), *Bot. Gaz.* *Triticum-Ægilops*, Kihara (1931, 1935), Kattermann. *Triticum-Secale*, Kattermann (1935), *Z.I.A.V.*; Ledingham and Thompson (1938), *Cytologia*. *Zea-Euchlæna*, Beadle (1932), *Genetics*; Mangelsdorf. *Iris*, Simonet (1935). *Tulipa*, Upcott and La Cour.

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